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ASPECTS OF REPRODUCTION IN THE MALE HUMPBACK WHALE, *MEGAPTERA NODOSA* (BONNATERRE)

By R. G. CHITTLEBOROUGH*

(*Manuscript received August* 2, 1954)

Summary

At puberty, male humpback whales off the Western Australian coast have an average body length of 36 ft 9 in. From histological examination of the testes, the extreme range of lengths at puberty is from 33 ft 4 in. to 40 ft 10 in. The mean testis weight at puberty is 2000 g. Following puberty, males are of low fertility for a period (possibly 1 yr) during which testis weight, tubule diameter, and spermatogenetic activity increase, before the attainment of full sexual maturity.

The mean length of the penis at puberty is 3.5 ft, but owing to considerable individual variation the penis length alone is not a reliable criterion of puberty. In sexually mature males the penis length ranges from 3.2 to 6.2 ft.

The proportion of fully physically mature males amongst those examined was very low (1.4 per cent.). The mean body length of those defined in this paper as approaching physical maturity was 41.90 ± 0.35 ft, and that of the fully physically mature males was 42.97 ± 1.59 ft. The largest male examined (46.42 ft) showed no sign of epiphysial fusion.

Changes in mean testis weight, mean diameter of testis tubules, and number of sperms in testes and vas deferens fluid have been followed at various stages of the life cycle. The variations of these characters in mature individuals have been examined for evidence of a seasonal cycle in male humpback whales; increasing testis weight and more active spermatogenesis are exhibited during winter months off Western Australia.

I. INTRODUCTION

In previous studies on the humpback whale and upon whales in general, the female reproductive cycle has received far more attention than have reproductive changes in the male.

The length of male humpback whales at puberty (an important characteristic in catch analyses) has not been accurately determined. In earlier research upon reproduction in whales (Mackintosh and Wheeler 1929; Matthews 1937, 1938*a*, 1938*b*; Nishiwaki and Oye 1948; Jonsgard 1951; Omura 1953) the term "sexual maturity" has been applied in a very general sense to mean that stage at which whales are capable of, and do effect, reproduction. In this paper it is intended to follow the procedure of Asdell (1946, p. 10), applying the term puberty to that stage at which reproduction first becomes possible, i.e. when germ cells are released, and confining the term sexual maturity to the time when the animal reaches

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its full reproductive power. It will be seen that in the male humpback whale there is a significant interval between these two events.

Matthews (1937) working on humpbacks, and Mackintosh and Wheeler (1929) on blue and fin whales, used testis "volume" to follow the increase in testis size with body length; their data showed a rapid increase in testis size at maturity. Matthews claimed that in humpback whales there was no correlation between testis size and body length after maturity.

Japanese workers (Omura 1953) have indicated that in humpback whales at "sexual maturity" the weight of testes is 2000 g, but Omura suggests that this figure may be too low as an index of "sexual maturity".

Matthews (1937) recorded a penis length of 1.25-2.5 m in mature humpback whales. Mackintosh and Wheeler (1929) state that in blue and fin whales the penis undergoes considerable growth at "sexual maturity" and suggested that the size of the penis might be a useful index of the state of maturity.

Little information is available upon physical maturity in male humpback whales. Matthews recorded the state of the epiphyses of 12 males, three of which were approaching physical maturity.

While Mackintosh and Wheeler noted great enlargement of the testis tubules in blue and fin whales at maturity, no actual tubule diameters were given. Changes in the size of testis tubules from late foetal stages until after maturity have not been followed in whales.

Some indication of a male sexual season in humpback whales was noted by Matthews (1937), who found no spermatozoa in the testes of four mature males taken off South Georgia (Antarctica) in December-March but some sperms in the testes of three males taken off South Africa in July and August. Mackintosh and Wheeler (1929) also found indications of a similar breeding cycle in male blue and fin whales. They found very few sperms in testis tubules all the year round, but more in May, suggesting a male sexual season of April to June. Using testis "volume" they found no evidence of an increase in testis size during the breeding season. Engle (1927) found no sperms or spermatida in the testes of three male humpback whales at Trinidad, California, in August, and suggested a seasonal sexual cycle in the northern Pacific with breeding occurring during the winter months.

It is now possible to review the evidence of a male sexual season in humpback whales using such criteria as testis weight, diameter of testis tubules, spermatozoa in the testis, and variations of sperm density in vas deferens fluid.

This material was collected at Western Australian shore stations during the catching seasons (between June and early October) from 1951 to 1953.

II. METHODS

In this investigation, testis weight was used as a more precise index of testis development than the estimated volume used by Mackintosh and Wheeler (1929) and by Matthews (1937). Each testis was weighed after removing the epididymis and attached membranes. There was little difference in weight between the left and the right testis. In each whale the mean weight of the left and right testes was recorded. These mean testis weights of individuals and not the total weight of the testis pair are used throughout this paper.

When considering the testis weights of specified groups of males it was found that the distribution of mean testis weights within each group was unimodal and positively skewed; hence the geometric mean of the individual mean testis weights rather than the arithmetic mean was used as providing the better estimate of the mean for each group.

Samples of testis tissue were fixed in Heidenhain's Susa fixative or in formol-saline, sectioned at 7 μ and stained with haematoxylin and eosin. Although the whales had almost invariably been dead for at least 3 hr before tissues could be preserved, fair histological detail could be obtained, even in those dead for 8 or 9 hr.

During the histological examination of each testis sample, the diameters of 20 seminiferous tubules were measured with an ocular micrometer and the (arithmetic) mean diameter of the tubules obtained. Also the average number of sperms per tubule section (7 μ thick) was found after counting the sperms in 20 tubule sections.

Samples of fluid were collected from the vasa deferentia of relatively fresh whales (dead 3-6 hr). A 2 ml sample of fluid was withdrawn from the vas deferens by means of a syringe and added to a tube containing 8 ml of 10 per cent. formol-saline (giving a 1: 5 dilution of preserved material). The corked tube was rotated to ensure a free suspension of sperms and also rapid fixation, after which the cork was sealed with wax. Before carrying out sperm counts upon these specimens in the laboratory, each tube was horizontally rotated for 3 min to resuspend the sperms. A small sample was mounted on a Neubauer haemocytometer slide and the count made under a phase contrast microscope. In most samples it was not found necessary to dilute the material any further, but in a few, epithelial cells were so numerous that further dilution was necessary in order to distinguish the sperms.

The state of physical maturity of these whales was determined from examination of the vertebral epiphyses, those males having all epiphyses fused to their respective vertebrae being classified as physically mature. As described by Mackintosh and Wheeler (1929) and Wheeler (1930), epiphysial fusion in whales begins in caudal and cervical vertebrae, extending forwards from the caudals more rapidly than back from the cervicals, so that the last epiphyses to be fused to the centra are those in the anterior thoracic region.

After exposure of the vertebral column the stage of epiphysial fusion was found by the method described by Wheeler. In the unfused state, the line of pearly white cartilage could be easily seen, but when fusion was taking place it was difficult to distinguish cartilage. In such instances, a small chip of bone across the epiphysial junction was placed over a slot in the flensing deck and lightly tapped. If the specimen broke directly along the junction with a smooth (though undulating) surface, this was classified as unfused but close to the point of fusion. When fusion was complete, such a fragment broke irregularly with a rough spongy surface, seldom along the line of fusion. This method was checked histologically, the microscopic examination agreeing very closely with the field diagnosis. Whales in which epiphysial fusion had begun but had not extended throughout the vertebral column were classified as approaching physical maturity.

III. PUBERTY

(*a*) *Histological Examination of Testes*

As stated by Mackintosh (1942) histological examination of the testes is the only unfailing method of determining the sexual state of a male whale. Figure 1 shows the mean testis weights and body lengths of 101 male humpback whales whose testes were examined histologically and so could be classified as sexually immature, at puberty, or mature. Immature testes (Plate 1, Fig. 2) had all seminiferous tubules closed or a few with lumina but containing no dividing spermatocytes. In testes at puberty (Plate 1, Fig. 3) the majority of tubules were open and contained some spermatocytes while closed tubules were not uncommon. In testes from mature males (Plate 1, Fig. 4) all tubules were open and various stages of spermatogenesis could be observed.

Figure 1 indicates that there is a wide range in body length at puberty, the extreme range being from 33 ft 4 in. to 40 ft 10 in. Hence it would be impossible to classify individual males as sexually immature or mature on the basis of body length alone. However, in comparison with the range of mean testis weights from all males examined (253-13,600 g), there is a relatively narrow range of mean testis weight at puberty (1500-3030 g). The geometric mean of the mean testis weights from the 11 males at puberty (shown in Fig. 1) is 1982 g. Only two immature males of the 101 shown had mean testis weights exceeding 2000 g (2122 and 2408 g respectively), while only one otherwise normal male having a mean testis weight below 2000 g (actual weight 1862 g) was post-pubertal.

In samples of vas deferens fluid from 51 males (see Table 8), sperms were found in only one where the mean testis weight was below 2000 g (actual mean weight 1830 g) and here the sperms were exceedingly rare. On the other hand sperms were present in all vas deferens samples from males whose mean testis weights exceeded 2000 g.

From the above considerations, the mean testis weight at puberty of humpback whales from the Western Australian coast is very close to 2000 g. This fact affords a rapid and relatively reliable means of distinguishing sexually immature males.

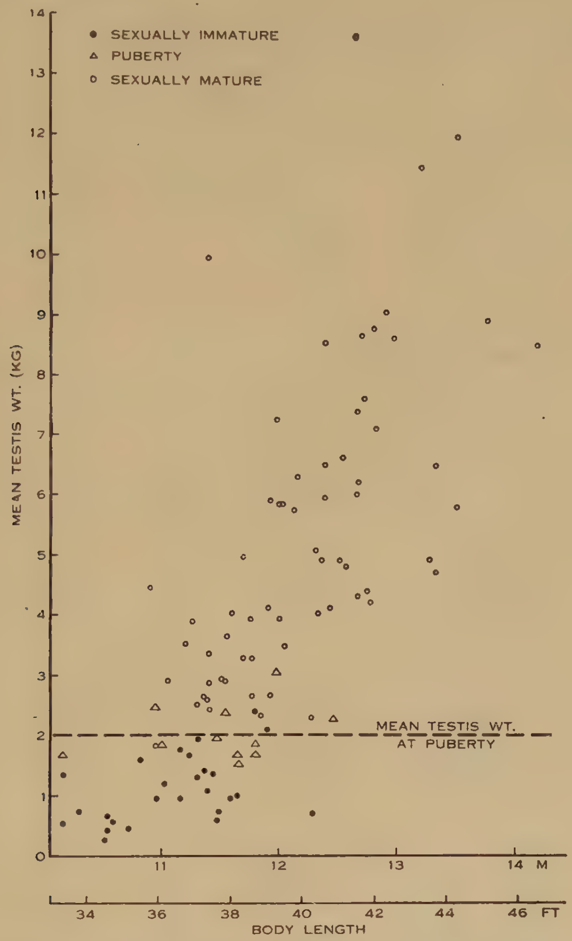

Fig. 1.—Testis weights (means of pairs) and body lengths of males whose testes were examined histologically.

(*b*) *Testis Weight*

Using the mean testis weight of 2000 g at puberty, the proportions of immature males in each 6-in. grouping of body length can be determined. Such a division on a basis of testis weight is shown in Table 1 for 609 males whose testes were weighed. The percentages of immature males in each 6-in. grouping of body length are shown in Figure 2. The curve in this figure indicates that at a length of 36 ft 9 in., 50 per cent. of male humpbacks would be sexually immature and 50 per cent. would have reached or passed puberty. This may be considered as the average length at puberty of male humpback whales.

TABLE 1

SEXUALLY IMMATURE MALES IN 6-IN. BODY LENGTH GROUPS, USING MEAN TESTES WT. OF 2000 G AS CRITERION OF PUBERTY

Body Length	Measurements Taken	Immature	
		Number	Per Cent.
ft in. ft in.			
30 0 to 30 5	1	1	100
30 6 to 30 11	—	—	—
31 0 to 31 5	1	1	100
31 6 to 31 11	1	1	100
32 0 to 32 5	—	—	—
32 6 to 32 11	1	1	100
33 0 to 33 5	7	7	100
33 6 to 33 11	7	7	100
34 0 to 34 5	3	3	100
34 6 to 34 11	11	11	100
35 0 to 35 5	10	9	90.0
35 6 to 35 11	15	10	66.7
36 0 to 36 5	11	8	72.7
36 6 to 36 11	22	10	45.5
37 0 to 37 5	24	10	41.7
37 6 to 37 11	29	7	24.1
38 0 to 38 5	31	8	25.8
38 6 to 38 11	42	3	7.1
39 0 to 39 5	54	1	1.9
39 6 to 39 11	44	0	0
40 0 to 40 5	46	2	4.3
40 6 to 40 11	49	0	0
41 0 to 41 5	47	0	0
41 6 to 41 11	40	0	0
42 0 to 42 5	42	0	0
42 6 to 42 11	24	0	0
43 0 to 43 5	16	0	0
43 6 to 43 11	12	0	0
44 0 to 44 5	7	0	0
44 6 to 44 11	6	0	0
45 0 to 45 5	2	0	0
45 6 to 45 11	2	0	0
46 0 to 46 5	1	0	0

Some confirmatory evidence of this length at puberty is adduced from Table 5, and from Figure 4, where the geometric means from the mean testis weights in 6-in. groupings of body length are shown. The geometric means from all length groups below 36 ft 6 in. are less than 2000 g, but those for all groups above this length exceed 2000 g.

(*c*) *Length of Penis*

Mackintosh and Wheeler (1929) suggested that in blue and fin whales the "size of the penis may be a useful means of deciding at a glance whether a whale is sexually mature or not, for this organ undergoes considerable growth at maturity". In the routine examination of hump-

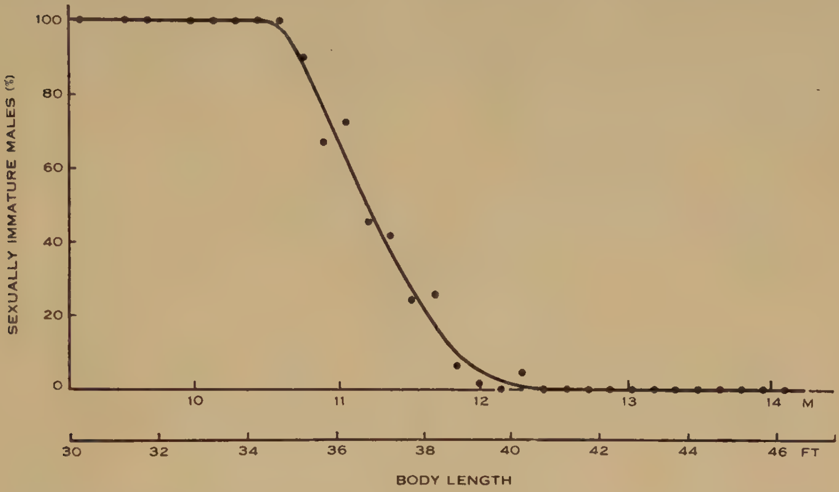

Fig. 2.—Proportions of sexually immature males in 6-in. groups of body length, using the mean testis weight of 2 kg as criterion of puberty.

TABLE 2

PENIS LENGTHS FROM MALES WHOSE TESTES WERE HISTOLOGICALLY EXAMINED

Immature		Puberty		Mature					
Body Length (ft)	Penis Length (ft)	Body Length (ft)	Penis Length (ft)	Body Length (ft)	Penis Length (ft)	Body Length (ft)	Penis Length (ft)	Body Length (ft)	Penis Length (ft)
33.33	2.92	33.33	3.58	35.75	4.33	39.08	3.92	41.50	4.58
33.75	1.67	35.92	4.00	35.92	4.42	39.08	4.50	41.50	5.17
34.58	3.67	36.08	2.75	36.25	4.75	39.25	4.25	41.50	5.25
36.17	3.58	37.58	4.17	36.75	3.75	39.33	4.25	41.58	4.25
36.58	3.25	38.17	4.08	36.92	3.17	39.33	4.42	41.67	3.83
36.58	3.75	38.17	3.67	37.25	3.83	39.42	4.50	41.75	5.33
36.83	2.58	38.67	2.17	37.33	4.58	40.33	4.33	41.92	3.58
37.08	2.67	39.25	3.42	37.42	3.50	40.42	4.50	42.00	5.00
37.08	3.67	40.83	3.42	37.83	3.75	40.50	4.67	42.25	4.75
37.25	2.92			37.92	3.67	40.58	4.42	42.50	4.58
37.50	3.50			38.00	4.25	40.58	4.83	43.25	4.75
37.58	2.67			38.33	3.83	40.58	5.17	43.50	4.25
38.00	2.17			38.50	4.08	40.75	4.33	43.67	4.83
38.17	2.42			38.58	4.08	41.08	3.83	43.67	5.00
40.25	3.25			38.83	4.25	41.42	4.75	44.25	4.75
				39.00	4.67	41.42	4.83	45.08	5.25
Mean: 2.98		Mean: 3.48		Mean penis length of 48 males: 4.41 ft					

back whales on the Western Australian coast, the length of the penis was recorded whenever possible. The penis was usually extruded when the whale was killed, but sometimes had been removed by sharks while the body was being brought into the station. The penis length of the mature humpback males examined range from 3.2 to 6.2 ft, which is considerably lower than that of 4.1-8.2 ft recorded by Matthews (1938*a*) from the same species in South Atlantic regions.

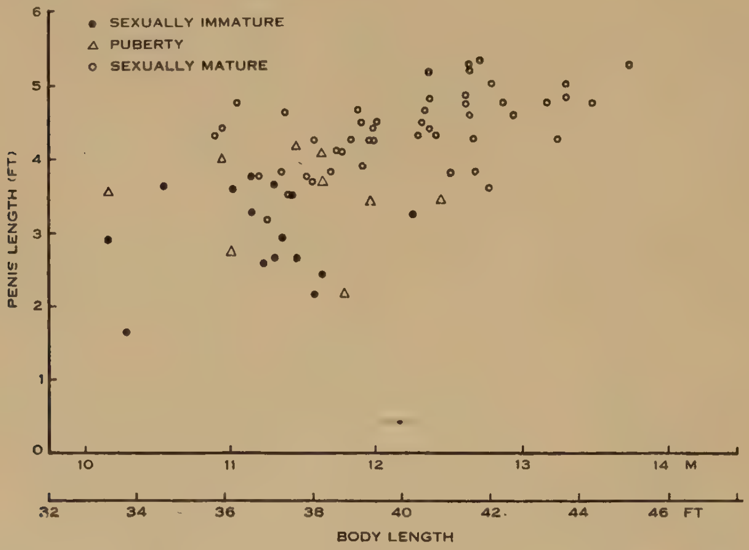

Fig. 3.—Lengths of penis and body lengths of males whose testes were examined histologically.

The penis lengths from 72 males, whose testes were examined histologically and so could be accurately classified as sexually immature, at puberty, or mature, are listed in Table 2 with body lengths. These records are plotted in Figure 3. There is some increase in penis length with increasing body length; this increase is slightly more rapid at puberty. Although males having a penis length of less than 3.5 ft (the mean length of the penis in males at puberty) were generally immature and those having a penis length exceeding 3.5 ft generally mature, a classification by means of penis length alone is not as reliable as that using a mean testis weight of 2000 g as an index of puberty.

It was found that the penis was often fully retracted (or sometimes only partially extruded) in immature males, while in almost all mature males it was fully extruded by the time the whale was hauled on to the flensing deck.

IV. Physical Maturity

Of 567 male humpback whales from the Western Australian coast where epiphyses were examined, 479 (83.5 per cent.) showed no epiphysial fusion, 80 (14.1 per cent.) were approaching physical maturity, while only 8 (1.4 per cent.) had attained physical maturity. The distribution of the body lengths of these males is shown in Table 3. The smallest male approaching physical maturity was 38 ft 5 in. in length, having epiphysial fusion up to the fifth lumbar vertebra, but this fusion may have been abnormal as there was a massive area of bone beneath the sixth and seventh lumbar vertebrae in this whale. The next males approaching maturity were two 38 ft 10 in. in length. On the other hand males of up to 46 ft 5 in. were found with no signs of epiphysial fusion. Total lengths and mean testis weights of males approaching, and at, full physical maturity are listed in Appendix I. These are summarized in Table 4.

TABLE 3

EPIPHYSIAL FUSION IN MALE HUMPBACK WHALES

Body Length	Total Examined	No Epiphysial Fusion		Fusion Begun		Full Fusion	
		No.	%	No.	%	No.	%
ft in. ft. in.							
Under 33 0	4	4	100				
33 0 to 33 5	7	7	100				
33 6 to 33 11	7	7	100				
34 0 to 34 5	3	3	100				
34 6 to 34 11	11	11	100				
35 0 to 35 5	10	10	100				
35 6 to 35 11	14	14	100				
36 0 to 36 5	11	11	100				
36 6 to 36 11	22	22	100				
37 0 to 37 5	24	24	100				
37 6 to 37 11	29	29	100				
38 0 to 38 5	25	24	96.0	1	4.0		
38 6 to 38 11	36	34	94.4	2	5.6		
39 0 to 39 5	46	45	97.8	1	2.2		
39 6 to 39 11	42	38	90.5	3	7.1	1	2.4
40 0 to 40 5	41	32	78.0	9	22.0		
40 6 to 40 11	45	38	84.4	7	15.6		
41 0 to 41 5	44	34	77.2	9	20.5	1	2.3
41 6 to 41 11	40	30	75.0	10	25.0		
42 0 to 42 5	38	25	65.7	11	29.0	2	5.3
42 6 to 42 11	24	15	62.5	9	37.5		
43 0 to 43 5	14	10	71.4	4	28.6		
43 6 to 43 11	12	6	50.0	5	41.7	1	8.3
44 0 to 44 5	7	3	42.9	4	57.1		
44 6 to 44 11	6	0	0.0	4	66.7	2	33.0
45 0 to 45 5	2	2	100				
45 6 to 45 11	2	0	0.0	1	50.0	1	50.0
46 0 to 46 5	1	1	100				
	567	479	84.5	80	14.1	8	1.4

The mean length at physical maturity is slightly above that at the onset of epiphysial fusion, but the fiducial limits for the former are wide.

TABLE 4

BODY LENGTH AND MEAN TESTIS WT. IN MALES NEAR AND AT PHYSICAL MATURITY

Stage of Development	Body Length (ft)				Mean Testis Wt. (g)		
	Min.	Max.	Mean	5% Fiducial Limits	Min.	Max.	Geom. Mean
Approaching maturity (80 males)	38.42	45.83	41.90	±0.35	2863	13,600	6352
At maturity (8 males)	39.83	45.50	42.97	±1.59	3660	11,230	6491

Although it is to be expected that the mean length at full physical maturity should be greater than that of those approaching physical maturity, a comparison of these two groups by means of the t test was inconclusive, as $t = 1.8$ on 86 degrees of freedom.

V. CHANGES DURING THE LIFE CYCLE

(*a*) *Testis Weight*

Table 5 shows the ranges and geometric means of the mean testis weights from 620 males in 6-in. body length groups and for several in the late foetal stages. Over the limited length range (12 ft 9 in. to 15 ft 5 in.) of the late foetuses whose testes were weighed, there is no evidence of any direct relationship between foetal body length and mean testis weight. Omitting these foetal records, the geometric means given in Table 5 are shown against body length in Figure 4. Included in Figure 4 are the geometric means of testis weights of humpback whales from the Antarctic reported by Omura (1953). These are considered in Section VI(*a*).

The testis weights from Western Australian coast humpback whales in Figure 4 show only a slight increase with body length during the greater part of the immature phase. Shortly before puberty, testis weight begins increasing more rapidly and continues to rise sharply for some time after this stage is reached. In larger (relatively older) mature males the variation in mean testis weight is considerable but independent of body length.

Figure 4 shows a group of very similar geometric means of testis weights between body lengths of 39 ft 6 in. and 41 ft 6 in. This break in an otherwise relatively regular rise in testis weight, occurring as it does in groups where the records are of high frequency (see Table 5), would be expected to be of some biological significance. Possibly this represents a young class of sexually mature individuals. The geometric means of the last five groups from the Western Australian series cannot be usefully discussed, the records in each being of low frequency and high variability.

TABLE 5

MALE HUMPBACK WHALES: RANGES AND GEOMETRIC MEANS OF MEAN TESTIS WEIGHTS

Body Length	Measurements Taken	Range (g)	Geom. Mean (g)
ft in. ft in.			
12 9 to 15 5*	11	22-56	36.3
30 0 to 30 5	1	—	253
30 6 to 30 11	0	—	—
31 0 to 31 5	1	—	291
31 6 to 31 11	1	—	262
32 0 to 32 5	0	—	—
32 6 to 32 11	1	—	553
33 0 to 33 5	7	365-1673	632
33 6 to 33 11	7	348-781	579
34 0 to 34 5	3	338-842	523
34 6 to 34 11	11	260-1695	604
35 0 to 35 5	10	480-2820	836
35 6 to 35 11	15	542-4455	1486
36 0 to 36 5	11	540-4512	1572
36 6 to 36 11	22	420-6520	2164
37 0 to 37 5	24	593-9045	2222
37 6 to 37 11	29	606-9945	2951
38 0 to 38 5	31	667-8575	3234
38 6 to 38 11	42	1095-8272	3982
39 0 to 39 5	54	1990-8925	4516
39 6 to 39 11	44	2275-10,850	5432
40 0 to 40 5	46	704-11,260	5698
40 6 to 40 11	49	2250-9770	5672
41 0 to 41 5	47	2315-13,600†	5609
41 6 to 41 11	40	2700-11,190‡	6350
42 0 to 42 5	42	3660-12,200	6597
42 6 to 42 11	24	4055-11,442	6533
43 0 to 43 5	16	2640-12,260	6713
43 6 to 43 11	12	4710-10,900	6765
44 0 to 44 5	7	5465-11,968	7812
44 6 to 44 11	6	4020-11,230	7843
45 0 to 45 5	2	8880-9995	9421
45 6 to 45 11	2	5095-8155	6446
46 0 to 46 5	1	—	8030

* Late foetal males.

† One record of 1018 g omitted as testes were definitely abnormal.

‡ One record of 673 g omitted as testes were definitely abnormal.

Males at physical maturity have mean testis weights very similar to males at the onset of epiphysial fusion, the geometric means being 6491 and 6352 g respectively (Table 4). These lie close to the geometric means of testis weights from corresponding groups of body length shown in Figure 4, in the region where testis weight is no longer rapidly increasing with body length. In Figure 5 the mean testis weight is shown against body length in each of 80 males approaching physical maturity. The range of testis weight is wide and there is no direct relationship between testis weight and body length in these males.

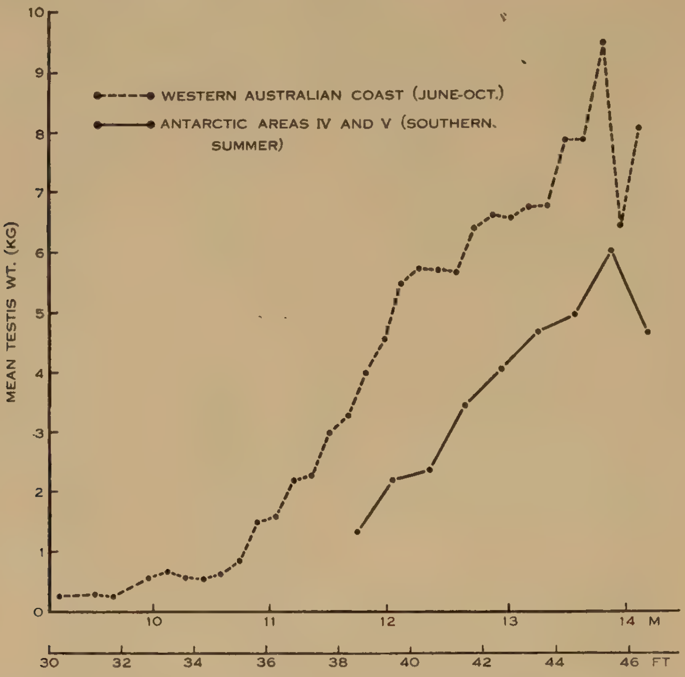

Fig. 4.—Geometric means of mean testis weights in 6-in. groups of body length. Japanese (Antarctic) records in 1-ft groups.

TABLE 6

MINIMA, MAXIMA, AND MEANS OF MEAN TUBULE DIAMETERS FROM TESTES IN FOUR STAGES OF LIFE CYCLE

Stage	Number Examined	Mean Dia. of Testis Tubules		
		Min. (μ)	Max. (μ)	Mean (μ)
Foetal	5	58	81	66
Immature	26	59	112	79
Puberty	11	87	121	103
Mature	65	108	199	155

(*b*) *Changes in Diameter of Testis Tubules*

The mean tubule diameters of 107 male humpback whales are shown against body length in Figure 6, each male being classified as late foetal, immature, at puberty, or mature. Table 6 shows the ranges and means of these mean tubule diameters for the four stages.

Figure 6 shows that there is very little increase in diameter of testis tubules from the late foetal stage until puberty. Yet there is an increase in mean testis weight from a mean of 36.3 g (in the late foetal stage) to nearly 2000 g during this period (see Table 5). During this phase of testis growth the testis tubules must increase considerably in length, but very little in diameter. In this regard it was noticed that there were more tubules crowded closer together in a given area of sections of immature testes than those of late foetal testes (Plate 1, Figs. 2 and 1 respectively).

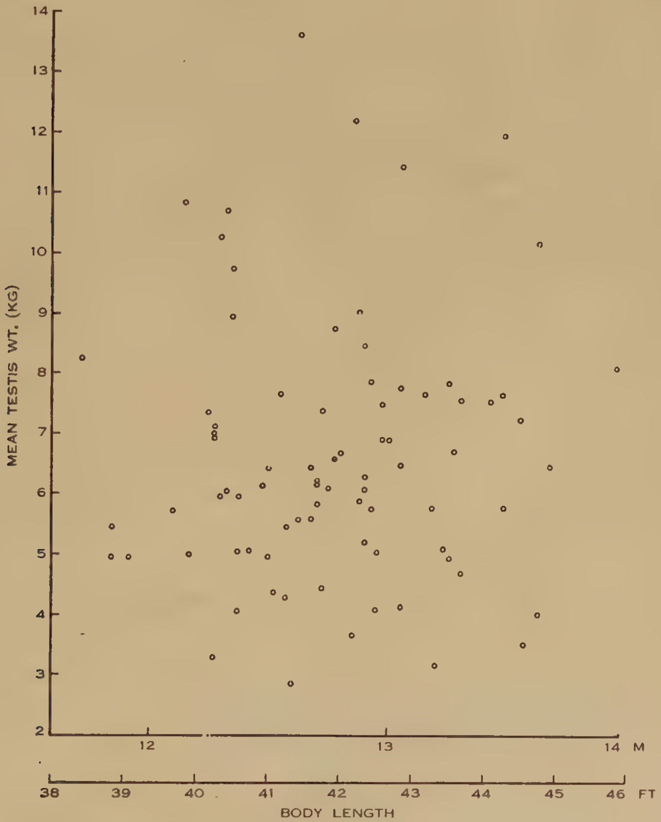

Fig. 5.—Mean testis weights and body lengths of males approaching physical maturity.

Two other differences between foetal and immature testes were noted. Firstly, sections of foetal testes showed more blood vessels (packed with erythrocytes) than those at any other stage. Secondly, in most instances the contents of the tubules of immature testes were shrunk away from the interstitium (see Plate 1, Fig. 2). This condition did not appear to be related to post-mortem changes nor to the methods of fixation, as it did not appear in foetal or mature material treated in the same way. At puberty the contents of the larger tubules with lumina were not shrunken from the wall (Plate 1, Fig. 3), while in other areas of the same material the smaller, inactive tubules were frequently of the same shrunken appearance as found in immature testes.

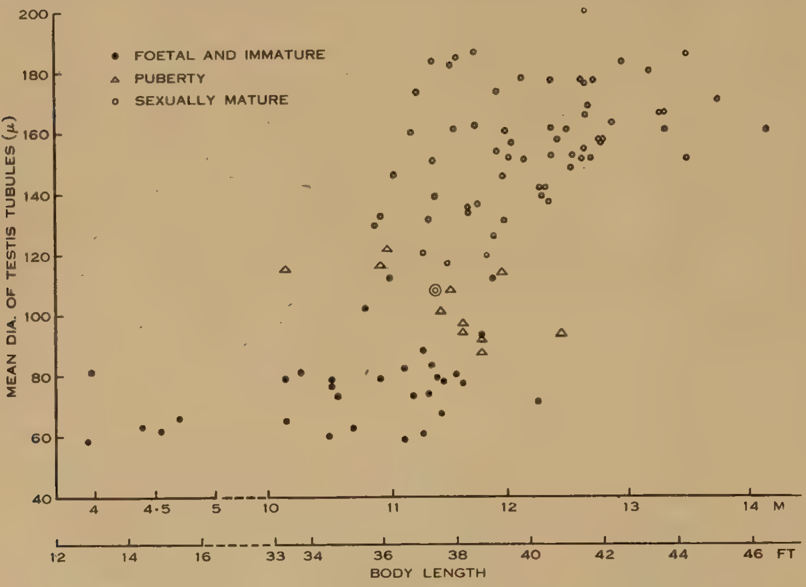

Fig. 6.—Mean diameter of testis tubules and body length of males at late foetal, immature, puberty, and mature phases.

Figure 6 demonstrates that at puberty there is a rapid increase in diameter of testis tubules. This change does not take place simultaneously in all tubules of a testis, some tubules enlarging suddenly, a lumen appearing with occasional dividing spermatocytes, while other tubules are still closed showing no signs of activity. An example of this type of activity is shown in Plate 1, Figure 3. Twenty measurements have been made both of inactive closed tubules and of open tubules in which spermato-

Table 7

Diameters of Closed and Open Tubules in the Testes of Four Males at Puberty

Dia. of Closed Tubules			Dia. of Open Tubules		
Min. (μ)	Max. (μ)	Mean (μ)	Min. (μ)	Max. (μ)	Mean (μ)
55	99	72	89	142	106
62	95	78	89	139	106
52	105	80	95	142	114
71	108	87	95	123	109

genesis was commencing in the testes of four of these males at puberty. These are summarized in Table 7.

Table 6 shows the mean tubule diameter from 11 males at puberty to be 103 μ, which is in fair agreement with the mean tubule diameters of the open tubules of the above four males where maturation of a few tubules had begun.

Figure 6 shows that the seminiferous tubules continue to increase rapidly in diameter for a period immediately after puberty, but that later there is little further increase in tubule diameter.

(*c*) *Spermatozoa in Testis Tubules*

The numbers of sperms in sections of testis tubules (cut at a thickness of 7 μ) vary to some extent, not only along one tubule but also between different tubules. However, the average number of sperms in 20 tubule sections selected at random does serve as an index of the relative activity of spermatogenesis in the testis.

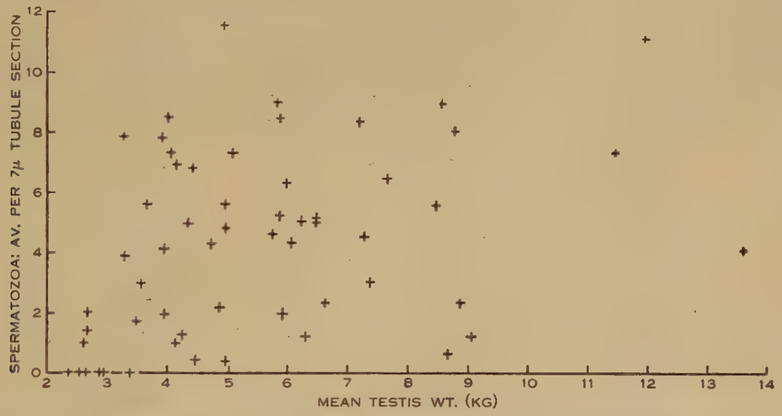

Fig. 7.—Average number of spermatozoa per testis tubule section (7 μ thick) and mean weight of testes.

Figure 7 gives the results of such sperm counts, the average numbers of sperms per tubule section (7 μ thick) being plotted against the corresponding mean testis weights. Numbers of sperms per tubule section are always relatively low in humpback whales. Mackintosh and Wheeler (1929) commented upon the paucity of sperms in the testes of blue and fin whales at all times of the year.

Figure 7 shows that shortly after puberty, when the mean testis weight is from 2000 to 3000 g, there are very few sperms in the testes. Sperms are more common in whales whose mean testis weights exceed 3000 g, but their number does not increase with testis weight.

Variation in the numbers of sperms in the testes during the months of June to October are discussed in Section VI(*c*).

(*d*) *Spermatozoa in Vas Deferens Fluid*

(i) *Density.*—The vasa deferentia in mature male humpback whales taken off the Western Australian coast in winter are generally swollen with seminal fluid, sometimes so much that some portions appear slightly bulbous. The results of the sperm counts upon vas deferens fluid from 50 male humpback whales are listed in Table 8, which includes the mean testis weight and total length of each whale and the date upon which it was killed. Sperms were present in the vas deferens fluid of only one

TABLE 8

SPERM COUNTS ON VAS DEFERENS FLUID

Mean Testis Wt. (g)	Sperm Density (10^6/c.c.)	Body Length (ft)	Date Killed
681	0	34.58	Sept. 3
704	0	40.33	Aug. 29
949	0	38.00	Sept. 3
1015	0	38.17	Aug. 5
1099	0	37.33	Aug. 29
1413	0	37.25	Aug. 14
1673	0	33.33	Aug. 27
1682	0	38.67	Aug. 5
1830	<0.250	36.08	Sept. 17
1846	0	38.67	Aug. 5
2597	1.250	37.33	Aug. 9
2630	0.250	37.25	Aug. 4
2664	0.375	39.08	June 18
3648	31.000	37.92	Sept. 4
3925	7.500	38.50	July 5
3930	7.250	39.33	Aug. 13
4016	87.500	38.00	Aug. 11
4045	19.500	40.42	Aug. 13
4125	15.500	39.00	Aug. 29
4135	97.000	40.75	Aug. 31
4220	36.500	41.83	Aug. 9
4420	32.500	41.75	Sept. 10
4710	26.000	43.67	Sept. 24
4830	6.000	41.17	June 11
4918	49.000	41.00	Aug. 12
4943	26.750	40.50	Aug. 7
4950	17.500	38.33	July 30
4960	83.500	43.50	Sept. 5
5080	68.250	40.33	Aug. 7
5740	164.250	39.75	July 30
5810	59.250	44.25	Aug. 3
5860	29.250	39.42	Sept. 25
5865	72.750	39.33	Aug. 13
5900	156.750	39.08	Sept. 19
5965	171.250	40.58	Sept. 23
6015	48.150	41.50	July 4
6213	104.775	41.50	Aug. 22

Table 8 (*Continued*)

Mean Testis Wt. (g)	Sperm Density (10^6/c.c.)	Body Length (ft)	Date Killed
6290	4.500	39.83	July 4
6483	24.000	43.67	Sept. 2
6498	86.000	40.58	Aug. 11
6935	89.000	40.25	July 10
7160	94.500	42.00	Aug. 28
7268	130.500	39.25	Sept. 23
7632	66.250	41.67	July 30
8480	78.000	46.42	Aug. 11
8545	41.500	40.58	July 11
8780	21.250	41.92	Sept. 29
9060	21.250	42.25	Aug. 4
11,968	175.000	44.25	Sept. 4
13,600	22.000	41.42	Sept. 10

male with a mean testis weight of less than 2000 g, and in this specimen only one sperm was seen. On the other hand, sperms were present in the vas deferens fluid of all males having a mean testis weight exceeding 2000 g. This supports the evidence in Section III (*a*) that the mean testis weight at puberty is 2000 g. In Figure 8 the density of sperms in vas deferens fluid is plotted against the mean testis weight for the males in Table 8, excluding those sexually immature. In the lower testis weight groups the density of sperms increases with the mean testis weight.

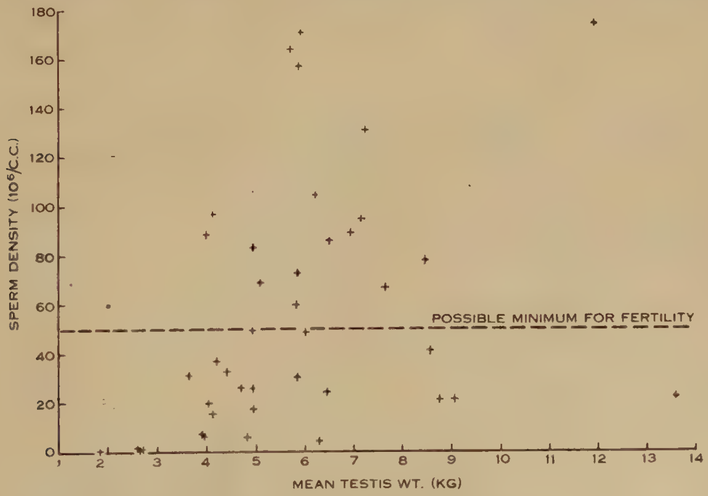

Fig. 8.—Density of sperms in vas deferens fluid and mean testis weight.

Neither the degree of dilution of fluid in the vas deferens on ejaculation, nor the minimum density of sperms required for copulation to succeed in conception is known in whales. However, if the density of 50×10^6 sperms/c.c. used by Harvey and Jackson (1945) as a criterion of fertility in human males is applied to the sperm counts in vas deferens fluid from humpback whales, most of those males having a mean testis weight of less than 5000 g would be classed as of low fertility, and the majority of those whose mean testis weight exceeded 5000 g would be (on a basis of sperm density alone) fertile. Some of the lower sperm densities in males of relatively high testis weight might be the result of copulation immediately prior to killing.

Very large numbers of epithelial cells were present in some samples of vas deferens fluid. These cells, roughly columnar and sometimes in small blocks, appeared to be degenerating, with little sign of nuclei even in the freshest material. Such cells appeared irregularly in seminal fluid with no apparent relationship to the presence or density of sperms.

(ii) *Morphology of Spermatozoa.*—Normal sperms from humpback whales are very similar morphologically to human sperms, having flattened oval-shaped heads 3-5 μ long. In total length they ranged from 32.2 to 64.4 μ with a mean length (from 50 measurements) of 52.5 μ. This may be compared with the total length of human sperms, given by Schafer (1949) as approximately 50 μ and by Maximow and Bloom (1948) as 61-62 μ. Sperm lengths have been recorded for two other species of Cetacea; Asdell (1946) quotes the sperms of the sperm whale as measuring 40.6 μ in length, and Retzius (1909) records that in the porpoise (*Phocaena communis*) the sperm head was 5.4-6.3 μ long and the total length of the sperm 73.8 μ.

In all samples of seminal fluid examined at least 80 per cent. of the sperms appeared to be normal, fulfilling the second criterion of Harvey and Jackson (1945) for fertility. In almost all samples a few abnormal forms were seen. These included the double, giant, and pin-head forms as well as double tail and thick neck types described by Harvey and Jackson in human semen. Such forms were included in the sperm counts listed above. Abnormal sperms did not appear to be present in different proportions in vas deferens fluids of low and high sperm density respectively.

VI. Evidence of Seasonal Activity in Mature Testes

(*a*) *Changes in Testis Weight*

For a comparison of testis weights in humpback whales at different periods of the year, individuals of the same age group should be used. While the precise ages of these males are not known, those approaching physical maturity (epiphysial fusion begun but not complete throughout the vertebral column) should be of approximately the same age. It is shown in Section V(*a*) that in males approaching physical maturity the mean testis weight is no longer increasing with body length. In Figure 9 the mean testis weights of 80 males approaching physical maturity are plotted against the dates upon which these whales were killed. Although few records are available in June, there is no evidence of any change in testis weight of these males between June and early October.

Omura (1953) recorded testis weights from humpback whales in the Antarctic areas IV and V. The geometric means given by him for 1-ft body length groups are shown in Figure 4 with the geometric means for 6-in. body length groups of males from the Western Australian coast. This shows that for males of corresponding body lengths, the testis weights from Antarctic individuals were always markedly less (24-64 per cent.) than those from Western Australian coast males.

On the evidence of testis weights from the Antarctic and from the Western Australian coast there is a seasonal variation in testis weights of mature humpback whales, with low testis weights in the Antarctic during the summer and much higher weights off the Western Australian coast during the winter and spring.

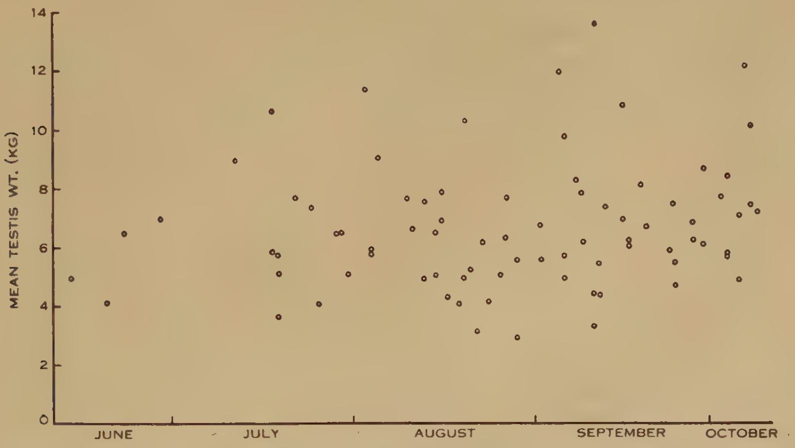

Fig. 9.—Mean testis weights of males approaching physical maturity and dates of killing.

(*b*) *Diameter of Testis Tubules*

In Figure 10 the mean diameters of the testis tubules from 64 mature humpback whales are shown together with the dates upon which the whales were taken. Smaller tubule diameters were more frequent in the testes of males taken in August than in other months. However, the majority of these lower mean tubule diameters were from younger males of shorter body length and lower mean testis weight taken soon after puberty, so that (as shown in Section V(*b*)) their testis tubules were still in a period of rapid increase in diameter. Disregarding the younger males with low mean tubule diameters which were of more frequent occurrence in August, Figure 10 gives no evidence of a cyclic variation in diameter of the testis tubules of sexually mature male humpback whales from June to early October.

(*c*) *Spermatozoa in Testis Tubules*

In Section V(*c*) it was shown that very few sperms were seen in the testis tubules of males having mean testis weights less than 3000 g, but that the greater numbers of sperms present when the mean testis weight exceeded 3000 g were independent of increasing mean testis weight.

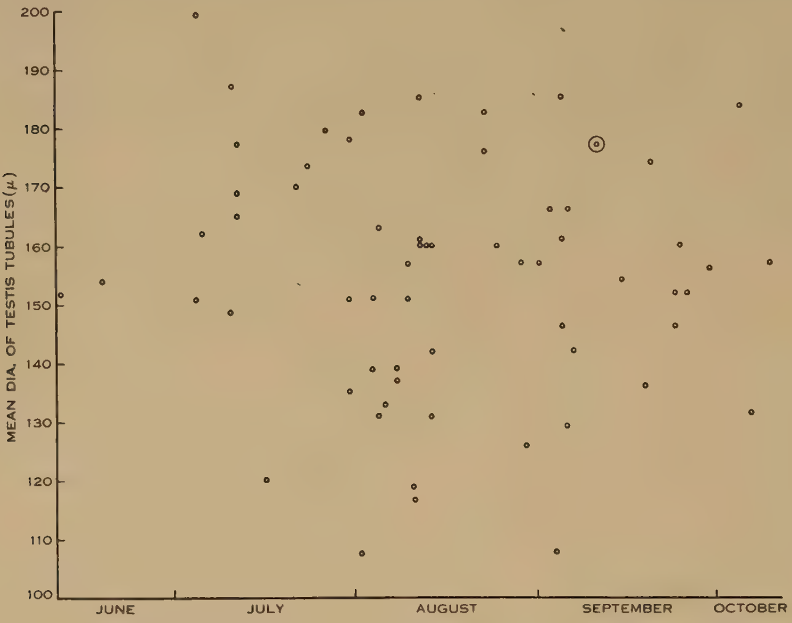

Fig. 10.—Mean diameters of testis tubules from mature males and dates of killing.

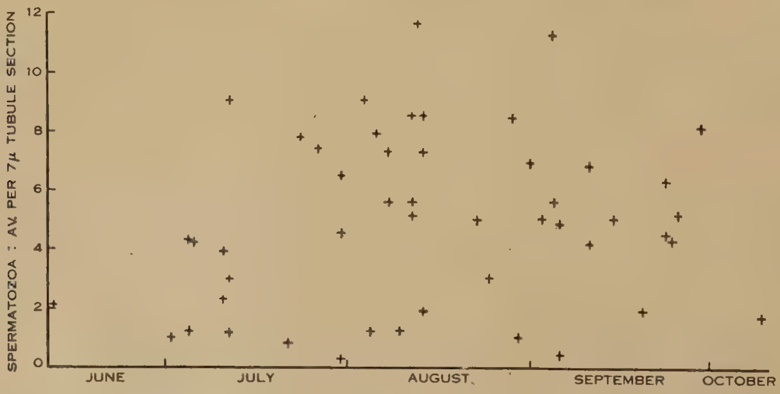

Fig. 11.—Average number of spermatozoa per testis tubule section (7 μ thick) of mature males whose mean testis weights exceeded 3 kg, and dates of killing.

In Figure 11 the average number of sperms per tubule section is shown against the date of killing for males whose mean testis weight exceeded 3000 g. Over the period when whales were taken (June to October), fewer sperms were present in the testes of mature males taken early in the season. Sperms were generally more plentiful in the testes of those taken in late July and August and, although still common in the testes of September killings, appeared to be a little below the peak of late July and August. Similar counts of sperms from the testes of male humpback whales taken in Antarctic regions would no doubt strengthen this evidence of a seasonal cycle of spermatogenetic activity, as Matthews (1937) found no sperms in the testes of four mature male humpback whales taken at South Georgia in December, January, and March.

(*d*) *Density of Sperms in Vas Deferens Fluid*

In Section V(*d*) it was shown that the density of sperms in vas deferens fluid tended to increase with mean testis weight up to 5000 g, after which there was no apparent relationship between sperm density and mean testis weight. In Figure 12 the densities of sperms in the vas deferens fluid of males whose mean testis weight exceeded 5000 g are shown with the times of killing. The records are insufficient to allow definite conclusions to be drawn but, considering the density of 50 × 10^6 sperms/c.c. tentatively used in Section V(*d*) as a criterion of fertility, the majority of those taken in early July would have been of low fertility, while from late July to September the greater proportion would have been fertile males (on this basis of sperm density alone).

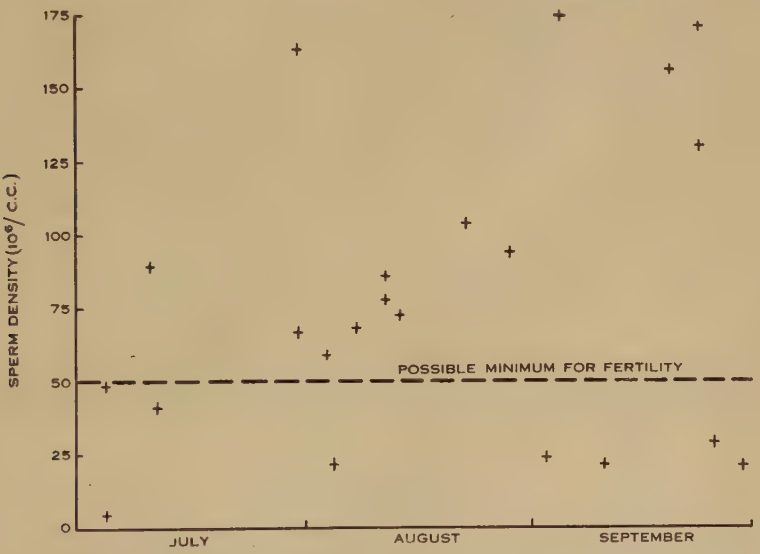

Fig. 12.—Density of sperms in vas deferens fluid of mature males whose mean testis weights exceeded 5 kg, and dates of killing.

In two successive years it was noticed while collecting vas deferens fluid that there was very often less fluid available from mature males taken in June and early July. Thus it is possible, by reason of low volume of semen and lower density of sperms, that mature male humpbacks are of lower fertility until late July. This conclusion is supported by the lower sperm counts on testis tubule sections in June and early July. Densities of vas deferens fluid taken from mature males in Antarctic areas would be of great value in any consideration of the seasonal cycle in male humpback whales.

VII. DISCUSSION

(*a*) *Puberty*

From histological examination of testes and analysis of mean testis weights it has been found that the average body length of male humpback whales from the Western Australian coast at puberty is 36 ft 9 in., with an extreme range from 33 ft 4 in. to 40 ft 10 in. Because of the relatively wide range in body length of individual males at this stage, body length alone is not sufficient to enable any one specimen within this range to be accurately diagnosed as having reached puberty. However, the average length of 36 ft 9 in. is important in catch analyses, offering a relatively reliable means of determining the proportion of sexually immature males in the yearly catch.

The mean testis weight of these males at puberty is 2000 g, so that the testis weight is a simple field guide (in the absence of histological methods) to the sexual conditions of individual males taken off Western Australia.

In this species puberty is generally reached at the end of the second year of life, but may sometimes be delayed until the end of the third year.

(*b*) *Sexual Maturity*

Following puberty there is a period of rapid increase in testis weight and diameter of seminiferous tubules. During this phase few sperms are present in the seminiferous tubules and the concentrations of sperms in vas deferens fluid are generally low. Such young males would be of suboptimal fertility. This indicates that sexual maturity (when full reproductive powers have been reached) is not attained until a further period, probably a year, after puberty.

(*c*) *Penis*

The size of the penis is not generally recorded in work on other groups of mammals, but Mackintosh and Wheeler (1929) noted that in blue and fin whales the penis increases considerably in size at "sexual maturity". In humpback whales the length of the penis increases with body length, with a more rapid increase at puberty. The mean length of the penis at puberty is 3.5 ft; the majority of males having a penis length of less than 3.5 ft are sexually immature, but the length of the penis alone is not a reliable guide. In the mature males examined the length of the penis ranged from 3.2 to 6.2 ft, which is considerably lower than that of 4.1-8.2 ft recorded by Matthews (1937) for the same species in South Atlantic regions.

(*d*) *Testis Weight*

After a slow rise during immaturity (when body length is fast increasing), testis weight begins increasing more rapidly shortly before puberty and continues to rise sharply for a period after this stage is reached. Later in life testis weights vary widely in individual males and show no relationship to body length. Similar increases in testis weights are recorded by Brody (1945) in man, by Robson (1949) in the bull, and by Jonsgard (1951) in the minke whale. Mackintosh and Wheeler (1929) obtained similar results with the volume of the testes of blue and fin whales.

TABLE 9

MEAN DIAMETERS OF TESTIS TUBULES FROM VARIOUS SEXUALLY MATURE MAMMALS

Species	Author	Number Examined	Mean Dia. of Testis Tubules Min. (μ)	Max. (μ)	Mean* (μ)
Polar bear	Knepp (1939)	1	—	—	105.8
Virginia deer	Knepp (1939)	1	—	—	139.4
Wallaroo	Knepp (1939)	1	—	—	141.1
Mouflon	Knepp (1939)	1	—	—	149.5
Humpback whale	Chittleborough†	65	108	199	155
Grey squirrel	Knepp (1939)	1	—	—	169.7
Cottontail rabbit	Knepp (1939)	1	—	—	173.9
Punjab wild sheep	Knepp (1939)	1	—	—	176.4
Man	Bascom and Osterud (1925)	1	—	—	183
Belgian hare	Bascom and Osterud (1925)	1	—	—	184
Albino mouse	Bascom and Osterud (1925)	3	191	201	194
Sheep	Bascom and Osterud (1925)	1	—	—	211
Dog	Bascom and Osterud (1925)	2	207	217	212
Pig	Bascom and Osterud (1925)	2	223	225	224
Guinea-pig	Bascom and Osterud (1925)	7	198	244	226
Bull	Bascom and Osterud (1925)	4	198	238	228
Albino rat	Bascom and Osterud (1925)	5	242	265	253

* Mean from all males examined.

† Present paper (Table 6).

(*e*) *Testis Tubules*

The mean diameter of the seminiferous tubules increases very little from the late foetal stage until shortly before puberty. At puberty some tubules begin enlarging, with development of a lumen and spermatocytes, before others show any change from the immature condition. The mean tubule diameter at puberty is 103 μ. Tubules continue to increase in diameter for a period after puberty (Fig. 6), later becoming more constant when males are sexually mature. Tubule diameters vary very little in different parts of a mature testis; for example, the mean tubule diameters from two samples of tissue from one testis were 161 and 159 μ.

Table 9 lists the mean diameters of seminiferous tubules from mature individuals of various mammals. Although the humpback whale has the largest testes of this series, the tubule diameter is relatively low. The size of the spermatozoa of the humpback whale is also within the range found in other species of mammals, the average length of sperms in this species being 52.5 μ.

While examining seminiferous tubules in sections of humpback testes it was noted that blindly ending branches were more common than in the testes of other mammals, for example, the rabbit (Huber and Curtis 1913) and man (Johnson 1934). In the humpback whale these branches were more common towards the surface of the testes, a single tubule leading to two short, blindly ending tubules of similar diameters to the original tubule. As such branching of seminiferous tubules is generally considered to be rare in mammals, this may be worthy of further investigation in the humpback and other species of Cetacea.

(*f*) *Sperm Concentrations in Vas Deferens Fluid*

Since it is not possible to obtain samples of ejaculatory fluid from whales, the vas deferens fluid has been examined. The concentrations of sperms in vas deferens fluid cannot be easily compared with those from ejaculatory fluid of other mammals, since in all species the sperms are diluted (sometimes greatly) on ejaculation by the secretions of accessory glands. The densities of sperms in vas deferens fluid from sexually mature male humpback whales taken off the Western Australian coast during July, August, and September ranged from 4×10^6 to 175×10^6 per c.c. with a mean value of 78.6×10^6 per c.c. This appears to be low for vas deferens fluid in comparison with the concentrations of sperms in ejaculatory fluid from the bull, ram, stallion, and boar (Perry 1952) and man (Harvey and Jackson 1945). However, in the Cetacea it is probable that there is less dilution of sperms on ejaculation, since vesiculae seminales and Cowper's glands have not been found in whales, though the prostate glands are present (Meek 1918; Ommanney 1932). Ommanney found that in the Cetacea the glands of the prostate are of primitive form, similar in arrangement to those in marsupials.

(*g*) *Physical Maturity*

The mean length of the physically mature males examined is 42.97 ± 1.57 ft and that of those approaching physical maturity (epiphysial fusion begun but not extending throughout the vertebral column) is 41.90 ± 0.35 ft, so that there is little further increase in body length once epiphysial fusion begins. The largest male whose epiphyses were examined was 46.42 ft in length and in this male epiphysial fusion had not commenced. No evidence has been found of any decline in testis weight or spermatogenetic activity in physically mature males.

Only 8 (1.4 per cent.) of 567 male humpback whales whose epiphyses were examined had reached full physical maturity. (Similarly, only 6 (1.8 per cent.) of 327 females were physically mature.) This very low proportion of physically mature males in a random sample of the catches off Western Australia from 1951 to 1953 might be due to one or more of the following causes: (i) such males might migrate farther offshore or not all move from Antarctic waters; (ii) physical maturity might be reached relatively late in life in humpback whales; (iii) owing to previous heavy fishing with a strong selectivity towards larger individuals, most of the physically mature animals may have been removed from the stock. At present there is no evidence to suggest that physically mature humpback whales differ from other individuals in their migratory habits. While it is considered likely that physical maturity is attained relatively late in life in this species, it would be of interest to compare the proportion of physically mature individuals in the Western Australian group with that in a less heavily fished population of humpback whales. This will be possible when the research begun by the Division of Fisheries, C.S.I.R.O., upon the humpback whales from the eastern Australian coast is further advanced.

(*h*) *Seasonal Cycle in Sexually Mature Males*

A cyclic variation in the weight or volume of testes from mature animals is generally accepted as sufficient to demonstrate seasonal sexual activity in males. Such a male sexual cycle has been demonstrated in a variety of mammals: moles (Asdell 1946), the hedgehog (Robson 1949), the water shrew (Price 1953), bats (Asdell 1946), deer (Wislocki 1949), the snowshoe hare, marmot, wood rat, prairie dog, and squirrels (Asdell 1946), the woodchuck (Robson 1949), the cottontail rabbit, ferret, stoat, and Siberian sable (Asdell 1946), and the fox (Rowlands and Parkes 1935). In the Cetacea, Meek (1918) has presented some evidence that the testes of the porpoise (*Phocaena communis*) undergo great development in the summer (northern hemisphere), the breeding season being in July and August.

In those species of whales which annually make long migrations from circumpolar feeding grounds to temperate and subtropical areas where the females undergo parturition and oestrus (see Mackintosh and Wheeler (1929) for blue and fin whales, Matthews (1937) and Chittleborough (1954) for humpback whales), a seasonal sexual cycle might also be expected in the males. Mackintosh and Wheeler were unable to demonstrate a seasonal change in testis volume from sexually mature blue and fin whales, but found sperms to be more plentiful in the testes of males taken off South Africa in May than in the testes of those taken in the Antarctic during summer months. With the humpback whale, Matthews found some sperms in the testes of three mature males taken off South Africa in July and August, but none in the testes of four mature males taken off South Georgia in December, January, and March. In the northern hemisphere, Engle (1927) found no sperms or spermatids in the testes of three male humpback whales at Trinidad, California, in August and from this suggested a seasonal cycle in the North Pacific with breeding occurring during the winter months.

In this investigation changes in testis weight, diameter of seminiferous tubules, numbers of sperms in testis tubule sections, and density of sperms in vas deferens fluid have been considered for evidence of a seasonal sexual cycle in male humpback whales. Using mean testis weights from males approaching physical maturity (approximately the same age), no regular variation in testis weight was found off the Western Australian coast during the months of June to October. However, testis weights recorded by Omura (1953) from males taken in the Antarctic in the summer were much lower than those from males of the same length taken off the Western Australian coast in winter (Fig. 4), indicating that a seasonal variation in testis weight does occur in sexually mature male humpback whales.

No evidence has been found of a cyclic variation in diameter of seminiferous tubules from mature males between June and October. Since testis weights are lower in summer individuals taken in Antarctic waters, the tubules might be of smaller diameter in this period, but no measurements are yet available. Cyclic variations in the size of the seminiferous tubules have been demonstrated in the ferret (Asdell 1946), but are better known in those species of birds (Watson 1919; Marshall 1949, 1950, 1951) in which the testes undergo great development during the breeding season.

Not only by the seasonal variation in testis weight, but also on the evidence of sperm counts in sections of seminiferous tubules between June and October (supported by the finding by Matthews (1937) of no sperms in the tubules of mature males in Antarctic waters during the summer) a seasonal cycle of testis activity can be postulated in mature male humpback whales. Spermatogenesis appears to be at a peak in late July and August, and though still active in September shows slightly less activity in this month. This agrees well with the ovulatory cycle in the female humpback whale, where it has been shown (Chittleborough 1954) that ovulation is of maximum frequency in late July, is still of frequent occurrence in August, and continues to occur in September to a lessened degree.

Variations in the concentrations of sperms in vas deferens fluid from sexually mature males taken off the Western Australian coast give some support to the evidence of an annual cycle of spermatogenetic activity.

However, since only the active part of the cycle can be studied here, counts of sperms in vas deferens fluid are required from males taken in Antarctic regions during summer months.

VIII. ACKNOWLEDGMENTS

The cooperation of the Norwest Whaling Company and the Australian Whaling Commission, enabling me to collect material at their respective shore stations at Point Cloates and Carnarvon, is gratefully acknowledged.

I wish to thank Professor H. W. Waring, Zoology Department, University of Western Australia, for advice and criticism and the University of Western Australia for the use of laboratory facilities; Dr. K. Sheard, Division of Fisheries, C.S.I.R.O., for reading the manuscript; and Mr. N. S. Stenhouse, Division of Mathematical Statistics, C.S.I.R.O., for assistance in the analysis of results. I am indebted to Mrs. M. Malcolm for many of the histological preparations.

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EXPLANATION OF PLATE 1

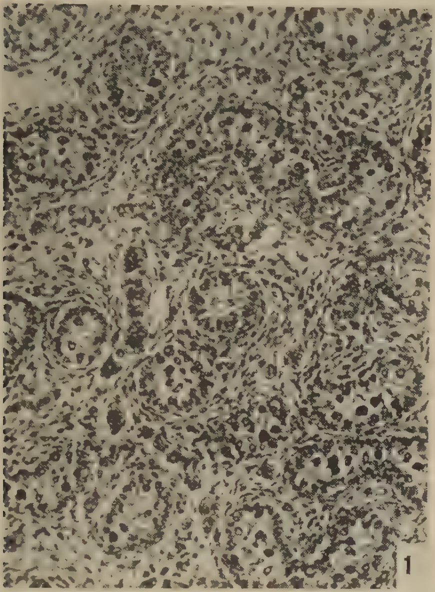
Fig. 1.—Section of testis from a late foetal male humpback whale. Body length 14 ft 11 in. Average tubule diameter 62 μ. Capillaries filled with erythrocytes common. × 125.

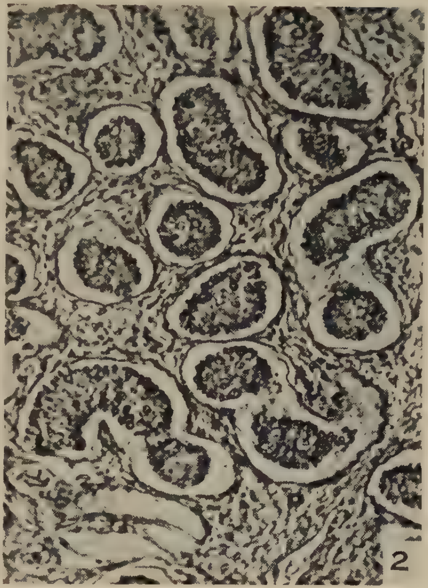
Fig. 2.—Section of testis from a sexually immature male. Average tubule diameter 73 μ. Shrinkage of tubule contents after fixation as commonly found in immature humpback testes. × 125.

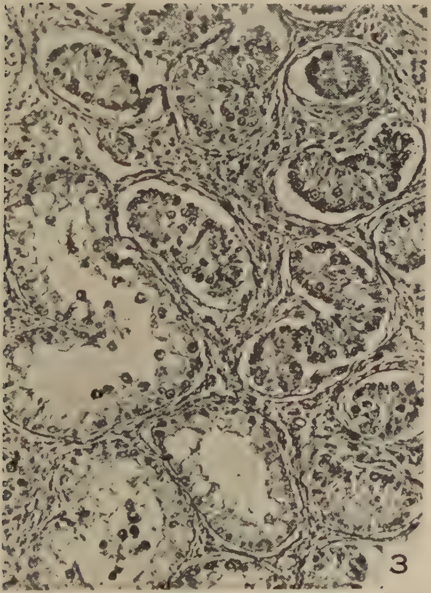
Fig. 3.—Section of testis from a male at puberty. Most tubules closed and contents shrunken from wall; average diameter 72 μ. Some tubules enlarging, with a lumen and few spermatocytes; average diameter 106 μ. × 125.

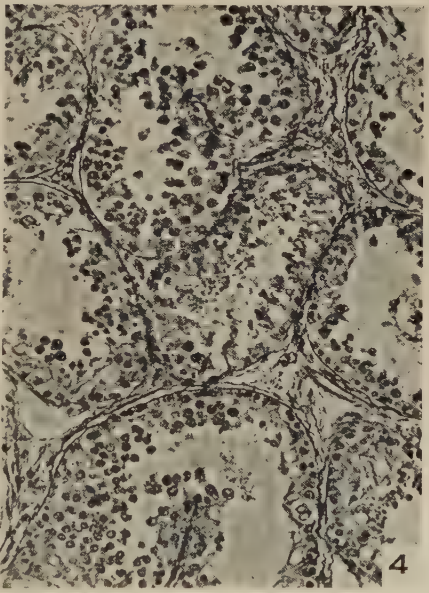
Fig. 4.—Section of testis from a sexually mature male taken during the breeding season. Average tubule diameter 160 μ. Spermatocytes, spermatids, and spermatozoa present. × 125.

REPRODUCTION IN MALE HUMPBACK WHALE









APPENDIX I

MALE HUMPBACK WHALES NEAR AND AT PHYSICAL MATURITY

(*a*) Epiphysial Fusion Begun but not Complete

Body Length		Mean Testis Weight (g)	Point of Last Fusion	Body Length		Mean Testis Weight (g)	Point of Last Fusion	Body Length		Mean Testis Weight (g)	Point of Last Fusion
ft	in.			ft	in.			ft	in.		
38	5	8270	5 Lumbar	41	3	4290	8 Thoracic	42	6	5035	3 Lumbar
38	10	4960	11 Lumbar	41	3	5460	4 Lumbar	42	7	6925	11 Lumbar
38	10	5465	7 Lumbar	41	4	2863	9 Lumbar	42	7	7505	10 Lumbar
39	1	4935	12 Lumbar	41	5	5588	10 Lumbar	42	8	6925	2 Lumbar
39	8	5735	8 Lumbar	41	5	13600	9 Lumbar	42	10	4133	11 Lumbar
39	10	10850	5 Lumbar	41	7	5590	12 Lumbar	42	10	6510	11 Lumbar
39	11	4975	10 Lumbar	41	7	6430	12 Lumbar	42	10	7780	9 Lumbar
40	2	7352	9 Lumbar	41	8	5825	9 Lumbar	42	10	11442	10 Lumbar
40	3	3285	10 Lumbar	41	8	6180	10 Lumbar	43	2	7660	9 Thoracic
40	3	6940	12 Lumbar	41	8	6235	12 Lumbar	43	3	5798	5 Lumbar
40	3	6990	11 Lumbar	41	9	4420	12 Lumbar	43	4	3180	10 Lumbar
40	3	7115	6 Lumbar	41	9	7370	12 Lumbar	43	5	5110	1 Caudal
40	4	5960	8 Lumbar	41	10	6115	11 Lumbar	43	6	4960	5 Lumbar
40	4	10293	11 Lumbar	41	11	6620	11 Lumbar	43	6	7850	5 Lumbar
40	5	6020	7 Lumbar	41	11	8775	12 Lumbar	43	7	6750	11 Lumbar
40	5	10712	11 Lumbar	42	0	6700	8 Lumbar	43	8	4710	1 Caudal
40	6	8955	1 Caudal	42	2	3662	12 Lumbar	43	8	7580	4 Lumbar
40	6	9770	11 Lumbar	42	2	12200	9 Lumbar	44	1	7545	10 Lumbar
40	7	4028	11 Lumbar	42	3	5895	11 Lumbar	44	3	5810	6 Lumbar
40	7	5015	11 Lumbar	42	3	9060	12 Lumbar	44	3	7660	8 Lumbar
40	7	5965	11 Lumbar	42	4	5210	11 Lumbar	44	3	11968	9 Lumbar
40	9	5058	7 Lumbar	42	4	6100	7 Lumbar	44	6	7210	10 Lumbar
40	11	6120	1 Caudal	42	4	6305	9 Lumbar	44	9	4020	10 Lumbar
41	0	4918	11 Lumbar	42	4	8490	10 Lumbar	44	9	10200	11 Lumbar
41	0	6428	11 Lumbar	42	5	5760	12 Lumbar	44	11	6490	1 Lumbar
41	1	4355	12 Lumbar	42	5	7870	9 Lumbar	45	10	8155	3 Caudal
41	2	7660	7 Lumbar	42	6	4065	9 Lumbar				

(*b*) Full Epiphysial Fusion

Body Length		Mean Testis Weight (g)	Body Length		Mean Testis Weight (g)
ft	in.		ft	in.	
39	10	5175	43	8	6482
41	3	7450	44	6	11230
42	2	3660	44	6	10800
42	4	5570	45	6	5095

EGGS AND LARVAE OF THE SABRE-TOOTHED OYSTER BLENNY, *DASSON STEADI* (WHITLEY) (BLENNIIDAE)

By I. S. R. MUNRO*

(*Manuscript received July* 26, 1954)

Summary

The eggs of the sabre-toothed oyster blenny, *Dasson steadi* (Whitley), are spawned in shallow pools between tide marks in estuaries. They are deposited in masses cemented in a single layer to the interior surfaces of discarded shells of bivalve molluscs. During development they are attended by the male parent. Hatching is spread over a prolonged period. The yolk-sac is absorbed about 1 week after hatching, by which time the larvae have developed functional teeth and ingest unicellular organisms. Egg and larval stages are described from naturally spawned material maintained under laboratory conditions for 17 days.

I. SOURCE OF MATERIAL

Several nests of naturally spawned eggs of the sabre-toothed oyster blenny, *Dasson steadi* (Whitley) have been obtained from the intertidal *Zostera* flats of Gunnamatta Bay, Port Hacking, N.S.W. In all instances the eggs were attached to the inner surfaces of shells of dead bivalve molluscs and guarded by a male parent. One example obtained on February 27, 1948, utilized the valves of the Sydney cockle, *Anadara trapezia* (Deshayes). Others obtained respectively on March 16, April 13, and July 28, 1953, occupied the valves of the razor shell, *Pinna menkei* (Reeve).

The nest that was collected on April 13 together with the attendant parent was placed in a large glass vessel of sea-water through which air was bubbled to provide oxygenation and circulation. The vessel was in direct sunlight and quickly developed a coating of green unicellular organisms. During 10 days under these conditions all the eggs hatched. On the 17th day all the larvae succumbed following the appearance in the vessel of a small area of anaerobic decomposition.

Whitley (1935)† has drawn attention to the spawning of this species in the Sydney district and the habit of the parent guarding eggs in an empty oyster shell.

II. CHARACTERS OF THE EGGS

In all observed instances the eggs had been deposited in a single layer, and disposed in irregularly shaped areas occupying several square inches on the inner surfaces of both upper and lower valves of the molluscan shells. The number of eggs appeared to be in proportion to the size of the parent and large fish chose larger shells for their nests.

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* Division of Fisheries, C.S.I.R.O., Cronulla, N.S.W.

† WHITLEY, G. P. (1935).—Some fishes of the Sydney district. *Aust. Mus. Mag.* 5: 291-304. 2 Pl.

Viewed from above (Fig. 1*B-E*) the outline of the egg is essentially circular except where flattened from being in close contact with a neighbour. The major diameter is in this plane and varies from 0.85 to 0.90 mm. In lateral profile (Fig. 1*A*) the eggs are sub-spherical with strong dorso-ventral depression. The base which is in contact with the substratum is slightly flattened, the sides broadly convex, and the top symmetrically domed. The height is 0.68-0.72 mm. The lower half, or more commonly the lower third, is tightly embedded in a cup of almost opaque fibrous material, whose substance forms a continuous layer over the substratum and serves to cement the eggs together as well as to the substratum.

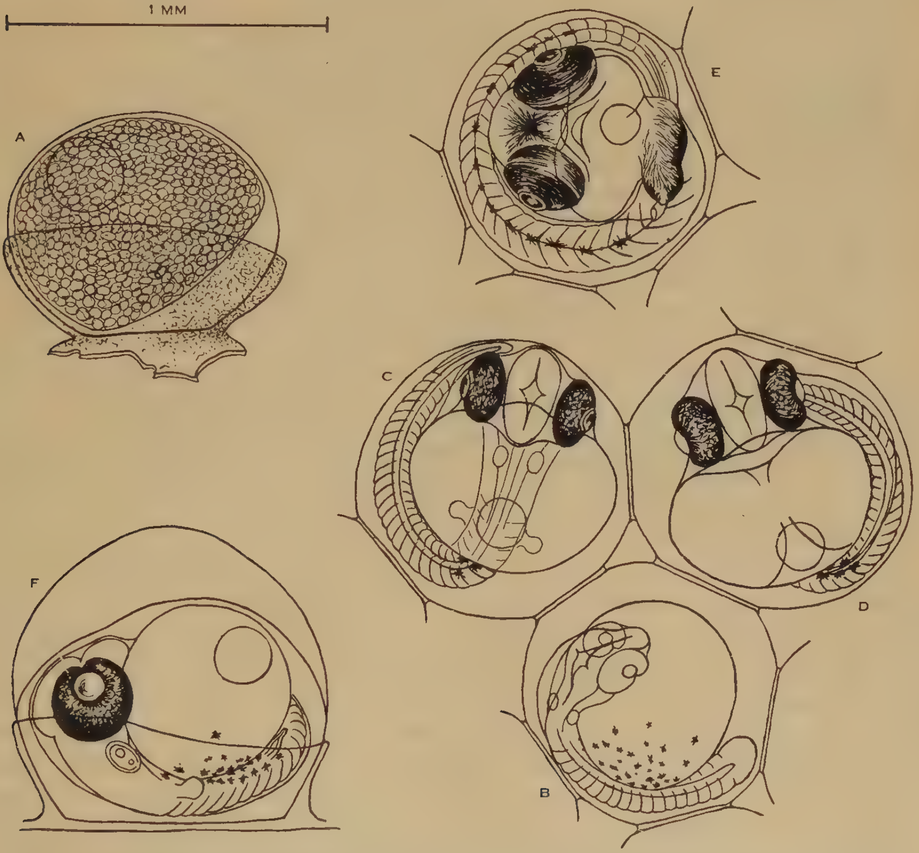

Fig. 1.—Eggs of *Dasson steadi* (Whitley): *A*, unfertilized egg with basal capsule (lateral view); *B*, early egg-embryo (viewed from above); *C-D*, more advanced egg embryos (viewed from above); *E*, egg embryo prior to hatching (viewed from above); *F*, egg with additional perivitelline structure (lateral view).

Some of the eggs (Fig. 1*F*) possessed an additional perivitelline structure in the form of a cushion over the dome of the egg, increasing the height to 0.93 mm.

The yolk substance is pale yellowish, hyaline, and composed of very large droplets. Within the yolk is a spherical aggregation of opaque granular material which measures 0.22 mm in diameter and occupies the position of a normal oil globule. Its presence is more obvious in preserved material and its diameter decreases as development progresses. The yolk lacks the bright red or purple pigmented bodies characteristic of eggs of certain other blennies (Fig. 1*A*).

III. Development of Egg Embryos

The earliest observed stage of development (Fig. 1*B*) is an early somatic division where 17-18 myotomes can be counted. The free caudal tip projects only slightly beyond the surface of the yolk. The brain shows little differentiation. The eyes have received a lens and possess a wide choroid fissure, but are entirely devoid of melanin. Auditory vesicles are present. The embryo lacks pigment but a number of small melanophores have appeared on the yolk in an area adjacent to the embryo.

More advanced egg embryos (Figs. 1*C-D, F*) have distinct fore brain, mid brain, and cerebellum. The eyes are now large with a shallow choroid fissure and are intensely black with a metallic iridescence. The auditory capsule contains two definite granules. The pectoral fin buds are clearly differentiated and a rudimentary hindgut is present. There are four precaudal and 24-26 caudal somites. Pigmentation is represented by a small area of melanophores on the yolk and a short ventral series along each side of the embryo.

Eggs that are ready to hatch (Fig. 1*E*) can be distinguished as those containing embryos with a long free extension of the tail composed of 29-31 somites, an increase in pigmentation, and a more highly organized digestive system. The yolk has been reduced considerably in bulk and its spherical opaque body is similarly diminished in size. The yolk-sac is now broader than long and is divided into lateral lobes. The postero-dorsal lining of the visceral cavity is pigmented with closely packed melanophores, the spidery processes of which spread downwards. There is a single enormous melanophore over the anterior border of the fore brain. At the junction of the caudal somites and the ventral fin fold are 14 or 15 small melanophores. Greater organization of the digestive system is apparent from the large mouth and the folding of the gut into loops.

Since observations are based on eggs which were collected some time after fertilization the full interval of egg development remains unknown. At the time of collection each nest contained eggs in several stages of advancement, suggesting the possibility of deposition or fertilization on different days. In two nests large numbers of larvae were released during the transference of the nest to the hatching vessel. Further numbers of larvae then hatched daily over a period of 10 days.

During the process of development the nest was occupied by the male parent, who continuously circulated water through the nest by fanning movements with his fins. He was not observed to leave the nest during the 17 days and apparently did not feed.

IV. Newly Hatched Larvae

Newly hatched larvae measure 2.85 mm and possess five pre-caudal and 30 caudal myomeres. The viscera and yolk constitute a compact mass in the anterior third of the body. The yolk is broadly expanded in the lateral plane. Pigmentation is essentially similar to that in advanced egg embryos. Melanophores are densely congregated over the posterior part of the visceral cavity and between the yolk and auditory capsules. Several small stellate melanophores are situated on the thickened base of the pectoral fin and a much larger one below the axilla. The frontal prominence of the head is marked by a single large melanophore or a group of smaller ones. There are approximately half as many melanophores as somites in the series along the ventral border of the tail. The fin fold of the unpaired fins is continuous, originating above the base of the pectorals and slightly constricted towards its posterior extremity. Skeletal elements support the large mouth which is without teeth (Fig. 2*A*).

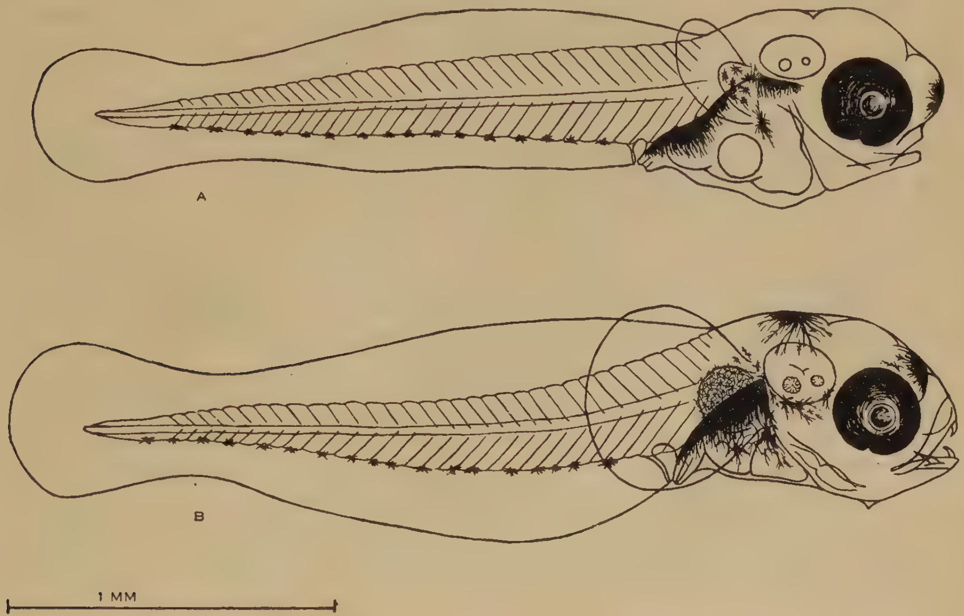

Fig. 2.—Larvae of *Dasson steadi* (Whitley): *A*, newly hatched larva, 2.85 mm; *B*, free-feeding larva, 3.00 mm.

V. Free-Feeding Larvae

Immediately after hatching the larvae congregated near the surface of the aquarium and were attracted to the side of the vessel nearest the window. In the course of about 1 week they began to leave the surface and feed at the bottom of the vessel by darting about and nosing in the film of green flagellates and ciliate protozoans. The presence of chlorophyll in the intestine of these larvae indicated that they were ingesting at least the flagellates and probably also the ciliates which were in close association. The canine teeth were by then functional and presumably served to scrape up organisms from the film on the bottom and sides of the vessel. These larvae were offered newly hatched nauplii of *Parartemia* but showed no interest in them as food although the latter did not appear too large to be swallowed.

These more advanced larvae, which measure 3.00 mm (Fig. 2*B*), possess five pre-caudal and 32 caudal somites. The yolk-sac is completely absorbed and its position occupied by a large liver and several loops of intestine. At this stage the anus and urinary pore are relatively further forward than when the larva emerged from its egg. There is some increase in the dimensions of the head, and the bones of the gill arches, opercles, and branchiostegals are easily distinguished. The auditory capsule is larger, is provided with chambers, and contains two relatively enormous spherulitic otoliths. An important feature is the appearance of dentition consisting of a pair of small symphysial canines in both upper and lower jaws, and a large pair of recurved post-symphysial canines in the lower jaw. There is some increase in the amount of pigmentation, especially in the peritoneal melanin and the areas of melanophores on the pectoral fin base and olefactory region. A patch of spidery melanophores has appeared over the cerebellum. In life the areas of melanin are shot with iridescent metallic colours.

STUDIES OF THE BLOOD AND TESTS OF SOME AUSTRALIAN ASCIDIANS

I. THE BLOOD OF PYURA STOLONIFERA (HELLER)

By R. Endean*

(*Manuscript received May* 5, 1954)

Summary

The blood cells of *Pyura stolonifera* are described and figured. Descriptions are given of the formation of the various cell types from the primitive lymphocytes of the blood. The presence of morula-shaped cells, which appear to correspond structurally with the vanadium-containing cells of members of the family Ascidiidae, is noted and the reaction of these cells to certain histological and histochemical reagents described.

Vanadium cannot be detected spectrographically in the ashed corpuscles but an iron compound with somewhat similar properties to the vanadium chromogen of the Ascidiidae is present. The iron is present in the ferrous condition and is capable of being liberated by acids. The iron compound has marked reducing properties and will reduce cytochrome *c* anaerobically. It is found in association with protein and an aminopolysaccharide. The importance of this association is discussed.

Investigations on the intracorpuscular acidity of the morula-shaped corpuscles reveal that, although acid is present, the hydrogen ion concentration is not as great as in the vanadium-containing cells of the Ascidiidae. This can be correlated with the lower intracorpuscular sulphate concentration of the present species. Analyses of the inorganic composition of the plasma show that the sulphate concentration is slightly over half that of the external sea-water.

The results of these and other investigations are compared with those obtained by workers using ascidians belonging to other families.

I. Introduction

There are some features peculiar to the blood and tests of ascidians that have aroused much interest and speculation. Firstly, there is the fact that some ascidians possess blood cells which contain a vanadium compound. Secondly, some blood cells contain free sulphuric acid which, at times, attains a concentration of 9 per cent. (Webb 1939*b*). The significance and function of the vanadium compound and of the sulphuric acid are not understood, nor is there general agreement as to the extent of the distribution of these substances within the Ascidiacea, despite considerable work on the subject (Henze 1911, 1912, 1913*a*, 1913*b*, 1932; Hecht 1918; Azéma and Pied 1930; Cantacuzène and Tchakirian 1932; Kobayashi 1933, 1935, 1938, 1949; Vinogradov 1934; George 1939; Webb 1939*b*; Pérès 1943; Califano and Caselli 1948, 1950; Bertrand 1950; Califano and Boeri 1950).

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* Department of Zoology, University of Queensland, Brisbane.

The third and perhaps the most outstanding idiosyncrasy of the Ascidiacea is the possession of a test composed of a substance called tunicin. In certain species, particularly those belonging to the family Ascidiidae, this tunicin as evidenced by biochemical and X-ray analyses appears to be identical with plant cellulose (Berthelot 1858; Winterstein 1894; Abderhalden and Zemplén 1911; Herzog and Gonell 1924; Meyer and Mark 1930; Spence and Richards 1940). However, Brien (1948), on the grounds that analyses of tunicin from some species have revealed a relatively high percentage of nitrogenous substances, stated that the composition of tunicin varies from species to species and is not identical with that of plant cellulose.

At least four different modes of formation of the ascidian test have been postulated (Brien 1930; Saint Hilaire 1931; Pérès 1945, 1948; Millar 1951). Possibly the method of formation varies from group to group within the Ascidiacea.

Fourthly, there are several types of corpuscles found in ascidian blood and, in many cases, little is known of their nature and function (George 1939; Webb 1939*b*).

It is the purpose of the present series of papers to record observations, analyses, and experiments made on the blood and tests of Australian ascidians which throw light on the above problems.

II. Materials and Methods

Pyura stolonifera is a common zoning animal which is found at low water along the coast of New South Wales (Dakin, Bennett, and Pope 1948) and which extends northwards along the Queensland coast as far as latitude 25°S. (Endean, Kenny, and Stephenson, unpublished data). Near Sydney, where work was commenced, there are two environmental forms of this species (Kott 1952). One (Fig. 1*A*) lives on rocky ocean shores whilst the other (Fig. 1*B*) is estuarine. The former was secured initially from Maroubra Bay, N.S.W., and subsequently from Currumbin, Qld. The estuarine form was obtained from Port Hacking, N.S.W. Both forms remained alive and apparently healthy for 2-3 days in a large, well-oxygenated tank of sea-water.

In both forms the fleshy portion of the animal is closely invested by a test which consists essentially of an inner layer of gelatinous material bounded by a thin layer of inorganic material consisting chiefly of sand grains. In the vicinity of the siphons and around the sides of the fleshy part of the animal the test is rarely more than 5 mm thick but below this region and extending down to the area of attachment to the substratum it is very bulky indeed (Fig. 2). Large blood-vessels enter this part of the test from the base of the fleshy portion of the animal and blood for biochemical analyses was obtained as follows:

(1) The bulky portion of the test was transected at approximately its mid point and the part containing test only discarded;

(2) A small depression was then made in the test surrounding the cut ends of the chief blood-vessels in the other portion and the animal inverted;

(3) The blood which welled up into the cup-shaped depression was withdrawn by means of a hypodermic syringe.

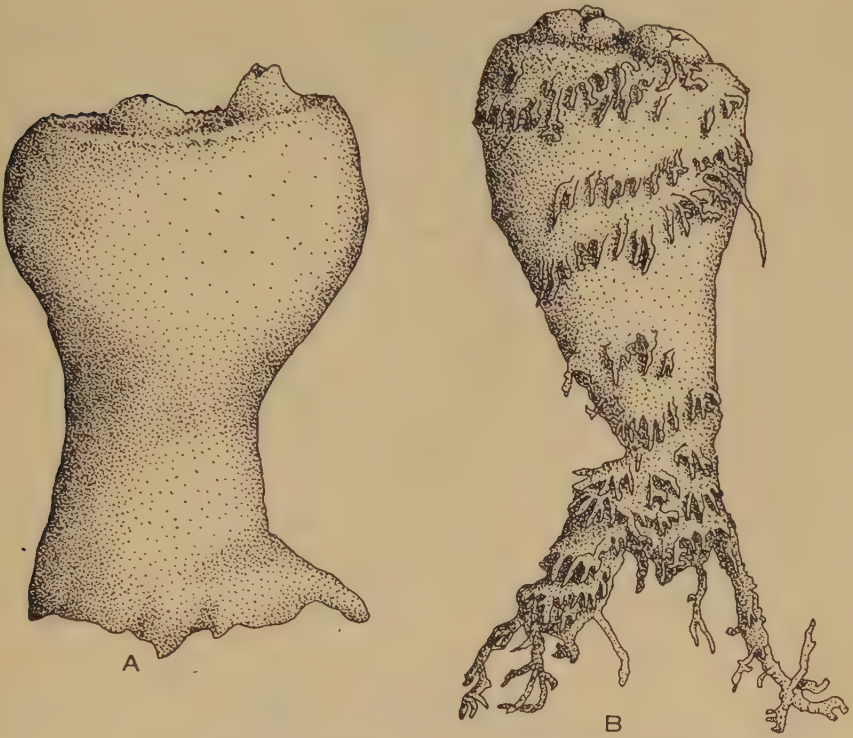

Fig. 1.—*A*, rocky ocean shore form of *Pyura stolonifera* × ½; *B*, estuarine form × ½.

From 20 to 60 ml of blood, depending on the size of the animal, could be obtained in this fashion from specimens of the rocky ocean shore form and up to 100 ml from very large specimens of the estuarine form. If required separately, plasma and corpuscles were separated immediately by centrifuging at 2000 r.p.m. Methods used in particular investigations are described under relevant headings.

III. Histology of the Blood Cells

(*a*) *The Blood Cells of Ascidians*

A great variety of cells, differing somewhat from species to species, is found in the blood of ascidians (Kollmann 1908; Fulton 1920; George 1926, 1930, 1939; Azéma 1929; Ohuye 1936). George (1939) has classified the common types of cells as follows:

(i) *Lymphocytes.*—The primitive cells of ascidian blood, giving rise to all other cell types and possessing large nuclei and a small amount of finely granular basophil cytoplasm.

(ii) *Macrophages.*—Found in all ascidians and are amoeboid, phagocytic, and contain numerous granules.

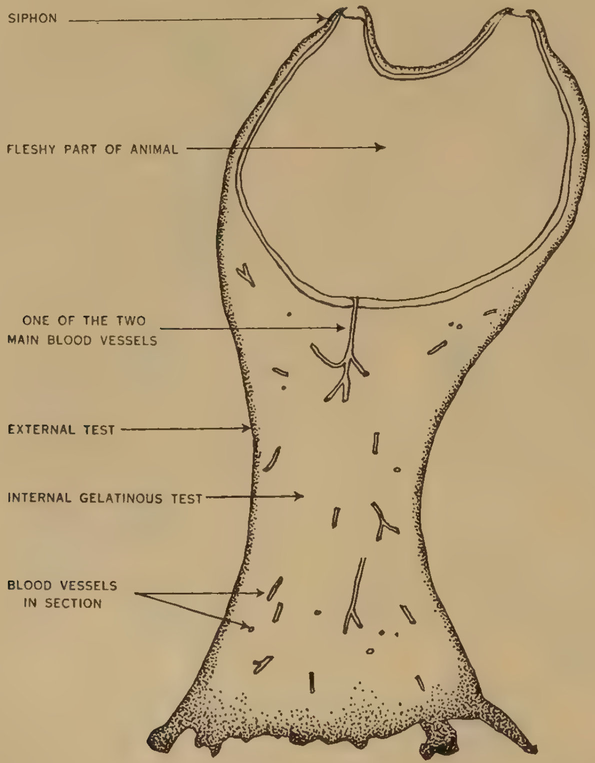

Fig. 2.—Sagittal section through rocky ocean shore form.

(iii) *Colourless Compartment Cells and Signet-ring Cells.*—Amoeboid, apparently structureless when unstained, with one or several vacuoles containing a fluid in which granules showing brownian movement are often present.

(iv) *Green Cells.*—George described these as "amoeboid berry-like cells with a greater or less number of spherical or mutually compressed globules of different sizes enclosed in colourless cytoplasm showing, when stained, a few scattered chromatin granules of moderate size . . . As a rule, though not always, they are coloured some shade of green".

(v) *Orange Cells.*—Amoeboid with coloured bodies, resistant to most chemical reagents, embedded in their colourless cytoplasm.

(vi) *Nephrocytes.*—The chief characteristic of this cell type is that it exhibits one colour by transmitted light and another by reflected light.

Its apparent function is to dispose of the waste products of purine metabolism.

(*b*) *The Blood Cells of* Pyura stolonifera

Haemocytometer counts on blood samples from 12 different specimens of the oceanic form gave a mean value of approx. 37,000 corpuscles/mm^3 of blood. However, there was great individual variation within a range of 18,250 to 68,200 corpuscles/mm^3. Counts on the blood of the estuarine form also revealed great individual variation in corpuscle count but this was consistently higher than in the oceanic form. The approximate mean value obtained was 43,000 corpuscles/mm^3 of blood.

The average volume occupied by the packed corpuscles from 10 ml of blood from the oceanic form approximated 0.1 ml. If an average diameter of 8 μ is attributed to the corpuscles (see (iv) below) the volume occupied by 37,000 of them would be in good agreement with this figure. Thus the corpuscles represent about 1 per cent. of the total blood volume.

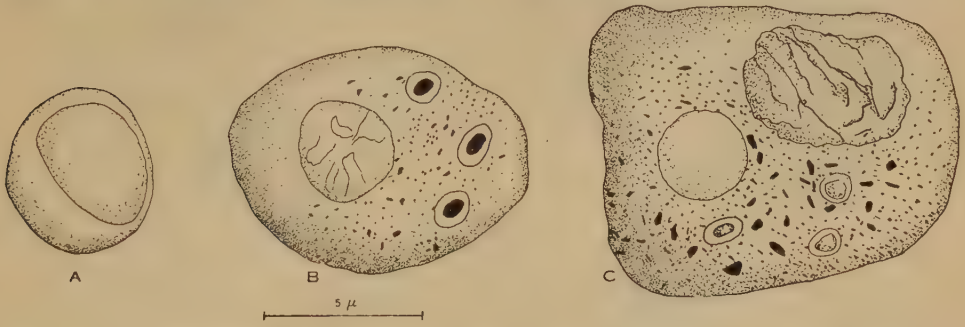

Fig. 3.—*A*, lymphocyte; *B*, transition stage from lymphocyte to macrophage; *C*, macrophage.

Blood from the oceanic form was then examined unstained in "hanging drop" preparations and after vital staining with neutral red and methylene blue. (Blood cells from histological preparations were also examined but these were so distorted that their examination contributed little to the elucidation of the structural features of each cell type.) The different types of corpuscles observed are listed below:

(i) About 5 per cent. of the total number of corpuscles consist of cells 5-6 μ in diameter (Fig. 3*A*). Their large nuclei, granular cytoplasm, and the absence of neutral-red bodies (cellular structures that stain intensely with neutral red) indicate that they would correspond with George's lymphocytes.

(ii) The next type of cell (Fig. 3*C*) could be placed in the macrophage category. These cells, in *P. stolonifera*, are 10-12 μ in diameter and comprise about 3 per cent. of the total number of corpuscles. They have abundant cytoplasm in which a few vacuoles and a large number of neutral-red bodies can be distinguished. Some of the larger neutral-red bodies are enclosed in a vacuole. Frequently they contain one or two ingested cells which have an orange tint.

(iii) Transition stages from lymphocytes to macrophages (Fig. 3*B*) are fairly common and can be recognized by the presence of large neutral-red bodies enclosed in vacuoles. The transitional lymphocytes gradually increase in size as a result of the production of more cytoplasm and small neutral-red bodies become increasingly numerous.

(iv) Morula-shaped corpuscles (Figs. 4*A*, 5*I*) are conspicuous in the blood and although their numbers fluctuate somewhat they usually comprise about 70 per cent. of the total number of blood cells. They are about 8 μ in diameter and there is little doubt that they correspond with Henze's (1913*a*) "maulbeerformen" and George's (1939) "green cells". The morula-shaped corpuscle of the present species consists of a number of spherical globules of variable size encased in colourless cytoplasm. A small excentrically placed nucleus is present but is usually obscured by globules. Although the morula-shaped corpuscles of *Ascidia mammillata* (Cuv.) as described by Webb (1939*b*), and those of *Pyura stolonifera* are of comparable size, the cells of the latter contain many more (12-38) but consequently smaller globules. These globules are distinctly greenish and show a great affinity for neutral red (0.0001 per cent. in sea-water). The stain was valuable in studying the cells both *in vivo* and *in vitro*. Probably the redness, which varies in intensity from cell to cell, is indicative of intraglobular acidity. When methyl red was added to a drop of the blood, a few of the morula-shaped cells became pale pink. However, as the drop began to dry around the edges, the corpuscles in that region ruptured and the exudate from the morula-shaped cells became deep red. Presumably the indicator was not able to penetrate the intact wall of the corpuscles.

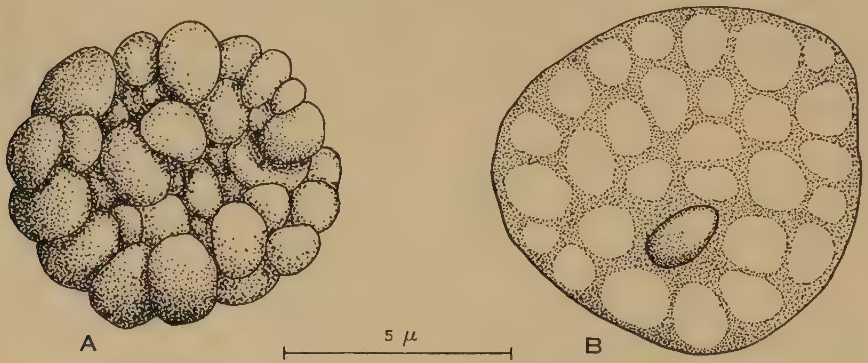

Fig. 4.—*A*, morula-shaped corpuscle; *B*, morula-shaped corpuscle after treatment with dilute acetic acid followed by methylene blue.

Dilute acetic acid dissolves the green intraglobular material and if methylene blue (0.0001 per cent. in sea-water) is subsequently added the nucleus and cytoplasm of the cell are stained (Fig. 4*B*). It can then be seen that the globules are separated from one another by thin, slightly granular, cytoplasmic extensions radiating from circum-nuclear cytoplasm.

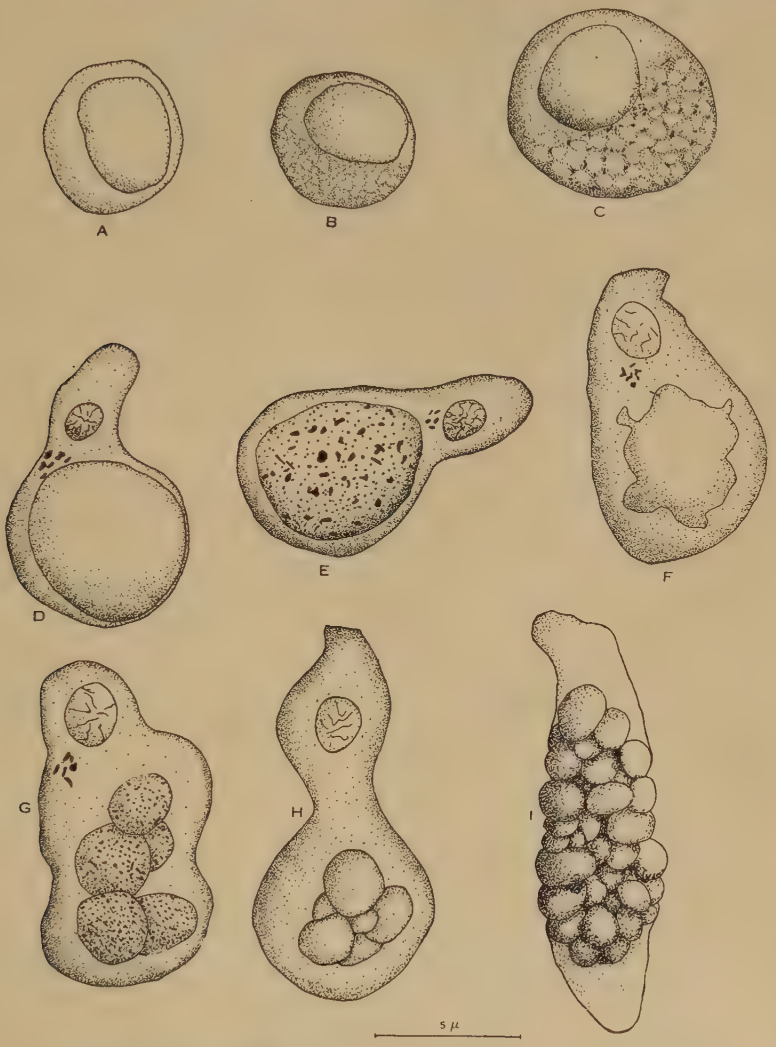

Fig. 5.—Transition stages from lymphocyte to morula-shaped cell. *A*, lymphocyte; *B*, lymphocyte with small vacuoles; *C*, enlarged lymphocyte with neutral-red bodies between the vacuoles; *D*, "signet-ring" cell; *E*, "signet-ring" cell with neutral-red bodies and granules in large vacuole; *F*, "signet-ring" cell showing "bubbling" of vacuole; *G*, cell with five vacuoles containing neutral-red bodies and granules; *H*, cell with six vacuoles each with layer of refracting material at their surface; *I*, morula-shaped corpuscle exhibiting amoeboid movement.

On the addition of water-soluble eosin, the globules stain reddish. They also give a grey colour with osmium tetroxide but never give a deep black colour with this reagent as with the morula-shaped cells of *A. mammillata* and other members of the Ascidiidae.

Observation of the morula-shaped corpuscles of *Pyura stolonifera*, using phase contrast microscopy, shows little because the globules overlie one another. After exposure to dilute (1 : 200) ammonia, however, they lose their surface refracting layer and often break free from the cell. Globules liberated in this fashion are seen, under phase contrast, to contain numerous granules suspended in a greenish-coloured fluid. Small globules are a deeper green than larger ones, indicating that possibly all globules contain about the same amount of greenish-coloured material.

The morula-shaped cells are capable of a considerable amount of amoeboid activity, which is more pronounced when blood stands a short time *in vitro* before examination. Single or multiple pseudopods are put out and may extend (as much as 10 μ) beyond the main mass of the cell. The globules do not enter the pseudopods initially but eventually pass into them. Cells which stain the darkest red with neutral red show the least pseudopodial activity.

(v) Transition stages from lymphocytes to morula-shaped cells are common in the blood and comprise about 20 per cent. of the total number of corpuscles. The transition seems to occur as follows:

(1) Lymphocytes develop small vacuoles between which numerous granules showing brownian movement appear (Fig. 5*B*).

(2) These vacuoles enlarge, as do the cells containing them, and between the vacuoles, which now assume a faint pinkish tinge with neutral red, angular neutral-red bodies appear (Fig. 5*C*).

(3) The small vacuoles then become enclosed in a large vacuole, the fluid in which stains pink with neutral red. Sometimes numerous neutral-red bodies and granules showing brownian movement are present in these large vacuoles (Fig. 5*E*). Usually the large vacuole appears to be devoid of these bodies (Fig. 5*D*) because of the presence of a surface layer of refracting material but, in both cases, vital staining with methylene blue shows that the small vacuoles and granules are still present within the large one — the dye staining the delicate cytoplasmic strands between these small vacuoles. The cytoplasm surrounding the vacuole appears structureless but near the nucleus, which at no stage is enclosed by the vacuole, there are always four to seven large neutral-red bodies. At this stage the cells, which are about 8-9 μ in diameter, probably correspond with George's "signet-ring" cells.

(4) The cells become very active and put out bulbous pseudopods in all planes. Frequently they fold upon themselves and there is much cytoplasmic streaming. The fluid within the vacuole then begins to "bubble" (Fig. 5*F*), some of the "bubbles" move out of the large vacuole, then snap back in again.

(5) The large vacuole then divides into two or more vacuoles which have a layer of refracting material at their surfaces (Fig. 5*H*). The globules slide over one another as a result of active protoplasmic streaming in the surrounding cytoplasm and appear to be identical with those of morula-shaped cells. They turn pink with neutral red and greyish when exposed to osmium tetroxide vapour. Such cells became typical morula-shaped cells as the result of the formation of more globules.

It is noteworthy that there is a gradual diminution in the size of the nucleus during the transition from lymphocyte to morula-shaped cell. Presumably, nuclear material is utilized. Also, in some cases, the formation of the surface layer of refracting material may be retarded considerably (Fig. 5*G*).

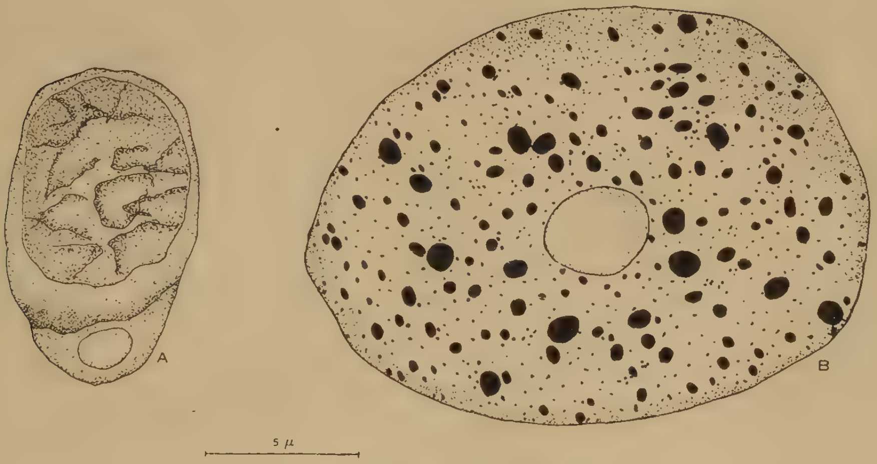

Fig. 6.—*A*, orange cell; *B*, nephrocyte.

Only the early stages of the transition from lymphocyte to morula-shaped cell as outlined above appear to correspond with George's (1939) account of the transition in *Ecteinascidia conklini minuta*.

Hence it is probable that this transition occurs via different routes — at least in the above two species.

(vi) Cells about 8 μ in diameter and each containing a large orange body with a granular appearance comprise about 1 per cent. of the total blood cells. The cytoplasm is folded at the end of the cell where the nucleus is situated (Fig. 6*A*). Presumably, such cells impart to the blood its orange colour and would correspond with George's "orange" cells.

(vii) Large cells, about 20 μ in diameter, are also found in the blood but make up less than 1 per cent. of the total blood cells (Fig. 6*B*). They are filled with dark bodies of various shapes, the larger being rounded in outline, and would fall into the "nephrocyte" category.

Corpuscles identical with those described above were found in the blood of the estuarine form. However, the morula-shaped cells in this form make up from 80 to 85 per cent. of the total number of cells and are thus present in greater proportion than in the blood of the oceanic form.

IV. CHEMISTRY OF THE BLOOD

(*a*) *Corpuscles*

The blood is slightly yellowish owing to coloured blood corpuscles. When separated from the plasma by centrifugation and allowed to stand exposed to air for a few minutes the bright yellow colour of the packed corpuscles changes to orange. Addition of fresh blood causes the yellow colour to reappear.

Chemical analyses made on the corpuscles were restricted to those with relevance to the chromogen present, the acidity of the intra-corpuscular material, and possible tunicin precursors elaborated by the corpuscles. Because of the difficulty involved in separating one type of corpuscle from another, chemical analyses were made on corpuscles of all types which were separated from the plasma by centrifugation. Of these corpuscles over 90 per cent. were morula-shaped corpuscles or their precursors. The contribution of all other cell types to the total intra-corpuscular material analysed is small yet cannot be neglected when evaluating the importance of some of the results obtained. However, in Section V substances detected as a result of these analyses are localized in certain cell types by histochemical means.

(i) *Action of Solvents, Acids, and Bases.*—Cytolysis with distilled water gave a lemon-yellow fluid which yielded an orange-brown precipitate. On the addition of alcohol or acetone a cloudy suspension appeared and sometimes a partial gel was found. Dilute sulphuric and hydrochloric acids turned the corpuscles reddish. Dilute ammonia produced a brown suspension and dilute sodium hydroxide produced a transient purplish gelatinous mass which soon yielded a brown precipitate.

(ii) *The Metal Chromogen.*—The presence of a vanadium chromogen in the blood of ascidians was first reported by Henze (1911). It was generally assumed that vanadium is present in the blood of all ascidians but the observations of Webb (1939*b*) indicated that vanadium was probably confined to a limited number of families — the Cionidae, Ascidiidae, and Diazonidae in particular. Bertrand (1950), however, found vanadium in all the species of ascidians he examined, although the metal was present in much greater concentration in the families mentioned above.

Since *P. stolonifera* possesses corpuscles resembling the vanadium-containing cells of the Ascidiidae, the vanadium content of the corpuscles was investigated. Blood from both oceanic and estuarine forms was centrifuged, the plasma discarded, and the corpuscles dry-ashed at 500°C.

The ash had a reddish brown colour. An attempt was made to estimate the vanadium content using the colorimetric method of Wright and Mellon (1937), but none was detected.

The ashed corpuscles from both forms were then examined spectrographically using a constant current D.C. arc, taking 5.6 A, and specially prepared vanadium-free carbon electrodes (Matthey Spectrographically Standardised Graphite Rods, No. 3053). The arc was placed 20 cm from the spectrograph slit and successive exposures, each of 15 sec duration, made of the emission spectrum between 2500 and 4000 Å. Exposures were made on the same plates of the emission spectra of standard iron and copper reference electrodes. The characteristic emission bands of vanadium at 3183.4, 3184, and 3185.4 Å were not detected. It was therefore concluded that vanadium is not present in the blood corpuscles of *P. stolonifera.*

Webb (1939*b*) did not find vanadium in *Tethyum partitum* (Stim.) or *Microcosmus sulcatus* (Coq.) — the two species of the family Pyuridae examined. It is possible that a vanadium chromogen is not present in the family Pyuridae.

Since copper and iron were present as impurities in the graphite electrodes, the copper and iron contents of the corpuscles were investigated in the following way. Eight sample lots, each of 20 ml of blood, from the estuarine form were centrifuged and the plasma removed; 5 ml of concentrated nitric acid and 2 ml of concentrated sulphuric acid were added to the corpuscles in each lot and the resultant suspensions heated until only a slight yellow colour remained, filtered through a sintered glass filter, and neutralized. Four filtrates were then tested for copper, using Sandell's (1944) sodium diethyldithiocarbamate method, but none was detected.

Another two filtrates were analysed for iron, using Sandell's (1944) *o*-phenanthroline method. A reddish colour was obtained with *o*-phenanthroline, indicating that iron was present. This was confirmed by acidifying the remaining filtrates with nitric acid and adding potassium ferrocyanide solution. Precipitates of Prussian blue were obtained. Similar results were obtained using corpuscles from the oceanic form. There are no previous records of iron having been found in the blood of ascidians.

In order to determine whether the iron was free or organically bound, the corpuscles from four lots of blood, each of 20 ml, were cytolysed with distilled water, filtered, and the filtrates tested for iron. None was detected and apparently the iron in the corpuscles is organically bound.

To determine whether the iron was in the ferrous or ferric state, the corpuscles from four 20-ml blood samples were taken and 5 ml of 6N hydrochloric acid added to each. The fragmented corpuscles were filtered off and the filtrates halved. Each half was tested with potassium ferricyanide and potassium ferrocyanide respectively. The iron was predominantly in the ferrous state. The concentration of iron in the corpuscles from 20-ml blood samples of 10 different specimens was estimated by Sandell's (1944) *o*-phenanthroline method. However, the optical density of the resultant coloured solution was measured with a Spekker absorptiometer using a blue-green filter (Ilford No. 603). A calibration curve was constructed using A.R. ferrous ammonium sulphate solution as standard.

Initially, the results were expressed on a blood volume basis and great individual variation in iron content was obtained. This could be correlated with great variation in corpuscle content. The mean value for the intracorpuscular iron content was 0.46 mg per cent. dry weight of the corpuscles with a range of 0.34-0.51 mg per cent. dry weight.

To investigate whether or not the iron compound was dialysable, blood corpuscles from 50 ml of blood were cytolysed with distilled water and the resultant suspension dialysed in a cellophane bag against distilled water in a beaker. After 24 hr the water in the beaker was tested for iron with potassium ferrocyanide. No iron could be detected and it was concluded that the iron compound is non-dialysable.

It was thought that the iron compound might be a respiratory pigment of the haem type. Examination of the blood with a microspectroscope, however, failed to reveal absorption bands and using the Beckmann spectrophotometer it was found that absorption was continuous over the range 400-700 mμ. A pyridine compound was then formed with human blood and the characteristic absorption spectrum noted. Using the same procedure an attempt was made to form a pyridine compound with the iron compound present in the corpuscles of *P. stolonifera*. Subsequent examination of the resultant suspension failed to reveal any absorption bands.

Thus there is a non-dialysable iron compound present in the corpuscles of *P. stolonifera*. The iron is present chiefly in the ferrous condition and is capable of being liberated, in part at least, by the action of acids. The iron compound does not seem to resemble haemoglobin at all closely.

(iii) *Reducing Properties of the Intracorpuscular Fluid.*—The iron-containing material released from the corpuscles following cytolysis with distilled water has marked reducing properties and will reduce, for example, potassium permanganate and potassium dichromate solutions. In this respect it resembles the behaviour of the vanadium chromogen, which is also a powerful reducing agent (Henze 1932; Webb 1939*b*). However, it differs from the latter in that it will not reduce methylene blue.

Califano and Boeri (1950) have shown that the vanadium compound of *Ascidia mammillata* will reduce cytochrome *c* both under aerobic and anaerobic conditions. The intracorpuscular fluid of *Pyura stolonifera* will also reduce cytochrome *c* anaerobically, as evidenced by the following experiment. The corpuscles from 50 ml of blood from the estuarine form were removed by centrifugation and cytolysed with 5 ml of distilled water. A few drops of 3×10^{-5}M cytochrome *c* from beef heart and 1 ml of 0.02M sodium succinate were added to the corpuscular suspension. No absorption bands were observed when the mixture was viewed through a microspectroscope. The mixture was then transferred to a Thunberg tube and the air in the tube replaced by pure nitrogen. After 5 min the mixture was again viewed through a microspectroscope and strong absorption bands characteristic of reduced cytochrome were observed.

Califano and Boeri (1950) noted that the cytochrome *c* which had been reduced by the vanadium chromogen slowly reverted to the oxidized form, even under anaerobic conditions, and that traces of catalase suppressed this reaction. A similar phenomenon was not observed in the present work. Presumably this is correlated with the fact that catalase was shown by the method of Humphrey (1943) to be present in the corpuscles of *P. stolonifera.*

(iv) *Intracorpuscular Acidity.*—Henze (1911, 1912, 1913*b*), working with *Ascidia mammillata* and *A. mentula* O.F.M., showed that sulphuric acid was present within the vanadium-containing blood cells and Webb (1939*b*) showed its concentration to be about 9 per cent.

The pH of both freshly-drawn blood and plasma of *Pyura stolonifera,* as determined by the glass electrode, was 6.7. After cytolysis of the corpuscles by freezing the pH of the blood fell to between 4.4 and 4.8. A similar result was obtained when the corpuscles were separated off by centrifugation, the plasma removed and replaced by an equivalent amount of distilled water.

Ten ml of blood after cytolysis required 2.7 ml of N/100 NaOH for its neutralization. Thus the acidity of the whole blood is 0.0027N. The only blood cells likely to liberate acid on cytolysis are the morula-shaped cells whose contents give an acid reaction with neutral red and methyl red. These cells occupy about 0.7 per cent. of the total blood volume and thus the acidity of the intracorpuscular fluid would be about 0.39N, or if the acid is sulphuric acid, about 1.9 per cent. H_2SO_4. Thus there is some acid present in the morula-shaped corpuscles of the present species but its concentration is far less than that of the intracorpuscular acid found in members of the Ascidiidae.

(v) *Intracorpuscular Sulphate.*—Henze (1912) determined the SO_3 content of the corpuscles found in the blood of *Ascidia mammillata.* Taking the average of his results it can be calculated that there is approximately 89 mg of intracorpuscular sulphate in 100 ml of the blood of this species.

Four pooled blood samples, each of 40 ml, of the blood of the oceanic form of *Pyura stolonifera* were centrifuged and the plasma removed.

Proteins present in the corpuscles were precipitated with 0.4 per cent. uranyl acetate and the precipitates removed by centrifugation. Attempts were then made to estimate the sulphate concentration of the supernatants, using the method of Letonoff and Reinhold (1936) which involved precipitation of the sulphate by benzidine. Inconsistent results were obtained but these indicated that the sulphate concentration was below 5 mg SO_4/100 mg dry weight of the corpuscles.

Webb's (1939*a*) barium iodate method for the estimation of sulphate in sea-water was then tried on the supernatants (it was necessary to obtain relationships between the amount of iodate released and the initial concentration of sulphate in standard sulphate solutions covering the range of concentrations expected in the supernatants). The results are expressed in mg SO_4/100 mg dry weight of corpuscles.

Sample	1	2	3	4	Mean
Mg/100 mg	3.7	3.4	3.6	3.4	3.5

Because of the possible effects of other substances present in the supernatant, on the final iodate concentration, the results can only be regarded as approximate. The dry weight of the corpuscles from 100 ml of blood of the oceanic form averages 230 mg. Thus there are approximately 8 mg of intracorpuscular sulphate in 100 ml of blood and this figure is much lower than that obtained for *Ascidia mammillata* as quoted above.

(vi) *Total Reducing Substances in Protein-free Corpuscular Extracts.*—Ten-ml blood samples were taken from each of 12 different individuals of the estuarine form. The corpuscles were removed from each sample by centrifugation and each made up to 5 ml with 25 per cent. trichloracetic acid. They were then centrifuged and the total reducing substances present in 0.1-ml samples of the protein-free supernatants estimated by the method of Folin and Malmros (1929). Blood samples from the oceanic form were treated similarly. In the estuarine form the mean of 12 determinations was 1.6 mg, expressed as glucose, in 100 mg dry weight of corpuscles. A range in concentration of 1.3-1.9 mg was found. The mean of 12 determinations made on the oceanic form was 1.3 mg with a concentration range of 1.1-1.6 mg glucose per 100 mg dry weight of the corpuscles.

Similar results were obtained when tungstic acid and uranyl acetate were used as protein precipitants. However, when zinc hydroxide was used no reducing substances could be detected in the supernatant and the centrifuged precipitate obtained consisted of two layers. The lowermost layer was brownish, and superimposed on this was a layer of gelatinous material similar to that obtained when alkali was added to the corpuscles. It seems probable that the gelatinous layer contains material which was precipitated by the alkaline protein precipitant and which is capable of reducing ferricyanide when in the free state.

Six 20-ml blood samples from six different specimens of the estuarine form of *P. stolonifera* were halved, centrifuged, and the plasma removed in each. Half the samples so obtained were then estimated for reducing substances as before. Each remaining half of the original samples was then hydrolysed by heating for 3 hr with 5 ml of 1N HCl in a boiling water-bath. Proteins were precipitated with 5 ml of 25 per cent. trichloracetic acid, and 0.1-ml samples taken and estimated for total reducing substances. Six 20-ml blood samples from six different individuals of the oceanic form were treated similarly (Table 1).

TABLE 1

TOTAL REDUCING SUBSTANCES IN THE BLOOD (MG GLUCOSE PER 100 MG DRY WT. OF CORPUSCLES)

	Oceanic Form		Estuarine Form	
	Unhydrolysed	Hydrolysed	Unhydrolysed	Hydrolysed
1	1.5	6.1	1.2	4.2
2	1.3	5.9	1.4	4.6
3	1.5	7.3	1.6	4.6
4	1.4	4.9	1.8	6.1
5	1.1	4.3	1.8	5.3
6	1.6	6.8	1.6	5.8
Mean	1.4	5.9	1.6	6.1

Thus in the oceanic form, total reducing substances have increased by an average of 4.2 times and in the estuarine form by 3.8 times the concentration prior to hydrolysis.

Similar results to the above were obtained when uranyl acetate, tungstic acid, and zinc oxide were used as protein precipitants after acid hydrolysis.

(vii) *"True" Sugar.*—Three samples, each consisting of the corpuscles from 10 ml of blood from the oceanic form, were hydrolysed by heating for 4 hr with 1N HCl in a boiling water-bath. HCl was removed by drying over NaOH in a vacuum desiccator. Proteins were precipitated with zinc hydroxide and the precipitates removed by centrifugation.

The supernatant in each case gave a strong Molisch reaction and reduced Benedict's reagent. Total reducing substances were then estimated in 0.1-ml samples as before and "true" sugar was estimated by the method of King and Garner (1947), which depends on the reduction of an alkaline copper solution, in 0.25-ml samples (Table 2).

Thus 98 per cent. of the total reducing substances present after hydrolysis of the corpuscles appears to be "true" sugar. It would seem, therefore, that a polymerized carbohydrate is present within the corpuscles. However, the methods used in Sections (vi) and (vii) were devised for use in investigations on mammalian blood. Although the iron-containing material was removed by the protein-precipitating agents used it is conceivable that in ascidian blood there are present substances, other than sugars, which will reduce the reagents used. Nevertheless in the next section it will be shown that a large proportion of the material released on hydrolysis of the intracorpuscular material is amino sugar.

TABLE 2

TOTAL REDUCING SUBSTANCES AND "TRUE" SUGAR IN THE BLOOD (MG GLUCOSE IN 100 MG DRY WT. OF CORPUSCLES)

	Total Reducing Substances	"True" Sugar
1	5.5	5.3
2	5.4	5.2
3	5.8	5.6
Mean	5.6	5.4

(viii) *Amino Sugars.*—Three samples, each of 20 ml of blood from different specimens of the oceanic form, were taken, centrifuged, and the plasma discarded. The corpuscles in each were then hydrolysed by heating with 5 ml of 6N HCl for 4 hr in sealed tubes in a boiling water-bath. HCl was removed by evaporation over solid NaOH in an evacuated desiccator. Amino sugars were then estimated by the method of Johnston, Ogston, and Stanier (1951). Results, expressed as mg of glucosamine per 100 mg dry weight of corpuscles, were:

Sample	1	2	3
Mg/100 mg	4.48	4.13	4.26

Thus there is an average of 4.29 mg of amino sugar expressed as glucosamine per 100 mg dry weight of corpuscles.

(ix) *Ionophoresis of Corpuscular Hydrolysate.*—Corpuscles from 50 ml of pooled blood taken from specimens of the oceanic form were cytolysed with distilled water. The mixture so obtained was then dialysed overnight with distilled water, hydrolysed with 6N HCl, and evaporated to dryness over NaOH as before. Activated charcoal was used to remove coloured material.

Aliquots of the hydrolysate were subjected to ionophoresis on filter paper using the method of Consden and Stanier (1952) and employing the apparatus described by Kunkel and Tiselius (1951). Sugars were detected by spraying the paper with aniline hydrogen phthalate (Partridge 1949).

It was found that the hydrolysate contained substances with mobilities corresponding to those of pure glucose and hexosamine. (The method does not distinguish between glucosamine and galactosamine. Because of the strength of the hydrolysing agent (6N HCl) used, the method as outlined is qualitatively unsatisfactory for sugars other than amino sugars, and the detection of glucose in the hydrolysate should be viewed with some suspicion.)

(*b*) *Plasma*

The plasma of *P. stolonifera* has an opalescent appearance. Estimation of the concentrations of Na, K, Ca, Mg, Cl, and SO_4 were made on the plasma of the rocky ocean forms and on the sea-water from the environment, using the methods of Robertson and Webb (1939) for all but the SO_4. This was determined by the barium iodate method of Webb (1939*a*). The results, which are each the means of three determinations, are expressed as mg/g of plasma and of sea-water respectively (Table 3). Depression of freezing point determinations on plasma and sea-water, following the method of Stephenson (1952), gave almost identical results.

TABLE 3

CONCENTRATIONS OF VARIOUS CONSTITUENTS AND DEPRESSION OF FREEZING POINT

	Na	K	Ca	Mg	SO_4	Cl	Δ F.P.
Plasma	10.56	0.40	0.45	1.44	1.38	20.49	2.03
Sea-water	10.97	0.41	0.44	1.42	2.66	19.97	2.01

Within the limits of experimental error, the concentrations of K, Ca, and Mg in plasma and sea-water are identical. The concentration of plasma SO_4, however, is only 52 per cent. that of the sulphate concentration of the external medium. This figure is similar to that (51 per cent.) obtained by Henze (1911) for *Ascidia mammillata.* Webb (1939*a*) working with the same species as Henze, obtained a figure of 61 per cent. but stated that the percentages obtained by both Henze and himself may be within the normal range of variation.

The plasma chloride concentration of *Pyura stolonifera* was 102.6 per cent. that of the external sea-water and the plasma sodium concentration 96.3 per cent. Because of the low sulphate concentration of the plasma the demands of electro-neutrality would probably account for the difference in chloride concentration observed — the higher chloride concentration being required to balance the cations.

As pointed out by Robertson (1949), ion concentration differences between body fluids and sea-water in osmotic equilibrium may be established as a result of deviations from the ideal laws of solutions and this may account for the low sodium figure obtained for the plasma. The reduction in sulphate concentration, compensated by an increase in chloride, necessitates a reduction in sodium because of the relatively greater osmotic effect of Na^+ and $SO_4^=$ ions in a solution of sodium sulphate.

On half saturating the plasma with ammonium sulphate, a small white precipitate was formed which increased slightly in volume as more ammonium sulphate was added, indicating the probable presence of albumens and globulins.

As determined with the glass electrode, the pH of the plasma was constant at 6.7. Rapkine and Damboviceanu (1925) found that the pH of the plasma of *Ascidia mammillata* was approximately neutral and this was confirmed by Webb (1939*b*).

V. HISTOCHEMISTRY OF THE BLOOD

(*a*) *Fixation*

Attempts to prepare blood smears, using techniques recommended for vertebrate blood, were unsuccessful. This may be due to the high salt concentration of ascidian blood and also to the fragility of the corpuscles, particularly the morula-shaped cells. The most satisfactory results were obtained by placing a drop of blood on a slide and adding 2 drops of 5 per cent. formalin in sea-water. Corpuscles were left for 2-3 min until pseudopodial action ceased. The blood and fixative were then smeared over the slide, using the edge of a coverslip, and the slide waved in air until the blood film began to dry around the edges. It was then flooded with distilled water before any salt crystallization occurred. Although a percentage of corpuscles was lost by this procedure, the remainder was suitably fixed.

(*b*) *Protein*

Smears, prepared as above, were flooded with Millon's reagent prepared after the method of Bensley and Gersh (1933). The corpuscles all became uniformly pink, indicating the presence of tyrosine-containing proteins. Arginine-containing proteins were also present in the corpuscles, as evidenced by the positive results obtained when Serra's (1944) method for the detection of these substances was employed. The morula-shaped corpuscles in particular contained considerable quantities of protein.

(*c*) *Lipoid*

Sudan IV and Sudan black *B* were added to formalin-fixed smears but none of the corpuscles took up the dyes nor was there evidence for the presence of lipoid in the intraglobular material released from cytolysed morula-shaped cells.

(*d*) *Polysaccharides*

Formalin-fixed smears were stained for polysaccharides by Hotchkiss's (1948) method. All types of cells gave a positive reaction but only the globules of the morula-shaped cells and the intraglobular material from cytolysed morula-shaped cells stained strongly. It was concluded that the intraglobular material contains polysaccharides.

(*e*) *Polysaccharide Sulphates*

Lison's (1935) method, which depends on metachromatic staining with toluidine blue, was used to test for the presence of polysaccharide sulphate compounds. The fixative recommended by Sylvén (1941) (equal volumes of basic lead acetate solution and 14-16 per cent. formalin) immediately cytolysed the morula-shaped corpuscles. However, some of the released globules were intact and these became red. The other corpuscles stained blue. It would appear that the intraglobular material of the morula-shaped corpuscles consists of a polysaccharide sulphate compound.

(*f*) *Iron*

As the presence of organically bound iron had been demonstrated in the corpuscles of *P. stolonifera* by chemical means an attempt was made to localize it histochemically using the Prussian blue reaction and Humphrey's (1935) dinitrosoresorcinol test. Macallum's (1908) nitric acid technique was used to convert the bound iron to the free form but proved too drastic to enable it to be used successfully on smears of the corpuscles. Formalin- and alcohol-fixed sections of the gelatinous test were therefore taken and the corpuscles in the blood-vessels of the test stained for iron with potassium ferrocyanide and dinitrosoresorcinol solutions respectively. Most of the morula-shaped cells and their vacuolated precursors stained positively for iron although there was considerable variation in intensity.

VI. Discussion

Henze (1913*a*) showed that the vanadium chromogen found in the blood of members of the Ascidiidae was confined to certain morula-shaped corpuscles. Webb (1939*b*) put forward evidence to show that such vanadium-containing cells (which he termed vanadocytes) were probably restricted to the Ascidiidae and Perophoridae. These vanadocytes were further characterized by their green colour *in vivo*, their marked reducing properties, and their high acidity.

In the blood of all other ascidian families so far studied, there are cells fundamentally similar in structure to vanadocytes. Usually these cells are coloured some shade of green but in some species they are colourless. George (1939) referred to all such cells as being of the "green-cell type". The question arises as to whether these cells carry a chromogen of some metal other than vanadium or none at all.

It has now been shown that the corpuscles of the green-cell type found in *Pyura stolonifera*, a member of the family Pyuridae, contain iron. Such corpuscles can be termed ferrocytes. They are green, as are the vanadocytes, but the green colour may be due to ferrous ions.

Vanadocytes give a deep black colour with osmium tetroxide. Henze (1913*a*) and Hecht (1918) believed that this blackening was due to the formation of a lower oxide of osmium as a result of reduction by the vanadium chromogen. Ferrocytes give only a greyish colour with osmium tetroxide and in this respect it should be noted that ferrous compounds are less powerful reducing agents than vanadous compounds.

On the other hand George (1939) noted that there was great variation in the intensity of the osmium tetroxide reaction exhibited by corpuscles of the green-cell type and suggested that this might indicate a variation in the percentage of fatty acids present in these cells. However, lipoids were not detected in the ferrocytes of *Pyura stolonifera.*

The iron-containing material of the present species and the vanadium chromogen of the Ascidiidae and Perophoridae have several features in common. Cytolysis of vanadocytes by distilled water gives a brown acid solution which has strong reducing properties but which slowly oxidizes on standing to give a blue-green precipitate. Cytolysis of ferrocytes by distilled water gives a lemon yellow solution which is slightly acid, has marked reducing properties, and oxidizes in air to give an orange-brown precipitate. In both, neutralization of the reduced form accelerates the production of the oxidized form of the pigment. Also the intracorpuscular vanadium-containing material of vanadocytes and the intracorpuscular iron-containing material of ferrocytes will reduce cytochrome *c* anaerobically. The importance of this characteristic is obscure.

Ferrocytes contain acid but the concentration of this acid is far lower than in the vanadocytes of *Ascidia mammillata* and *Ascidia mentula.* The acid present in vanadocytes is sulphuric acid and consequently there is a high intracorpuscular sulphate content. The lower acidity of the ferrocytes therefore may perhaps be correlated with the lower intracorpuscular sulphate concentration observed.

As regards the role of the H_2SO_4 in vanadocytes, Webb (1939*b*) stated that the properties of the vanadium chromogen were such "that a very acid medium is required to prevent it from being oxidized by dissolved oxygen". The truth of this statement is borne out by the work of Califano and Boeri (1950), who have shown that a pH of at least 2.4 is necessary to keep the vanadium chromogen in the reduced state. Likewise the presence of acid seems to be necessary to keep the iron-containing material of ferrocytes in the reduced condition.

All ascidians so far studied have a low plasma sulphate content, yet there are no known excretory organs in ascidians which could serve for the purposes of ionic regulation. Webb (1939*b*), taking into account the high intracorpuscular SO_4 content of vanadocytes, suggested the possibility of the low plasma SO_4 concentration resulting from a dynamic equilibrium in which SO_4 ions are taken from the plasma by the corpuscles and replaced by diffusion through the walls of the branchial capillaries. In the present species the free intracorpuscular SO_4 content is very low and unless SO_4 ions entering the corpuscles are quickly and effectively removed from solution by chemical union such a mechanism could not operate.

Apart from the presence of a vanadium chromogen and sulphuric acid the chemical nature of the intracorpuscular material of vanadocytes is not known, although it has frequently been stated that vanadocytes contain lipoid (Cuénot 1891; Kollmann 1908; Duboscq 1918). However, as Webb (1939*b*) pointed out, these cells do not stain with such fat stains as Sudan III, Sudan black *B,* or Scharlach *R.*

As regards the chemical nature of the intracorpuscular material of cells of the "green-cell type" belonging to other families little is known. Spek (1927) drew attention to certain "tropfenzellen" in the blood of *Clavelina lepadiformis*. These cells, which appear to belong to George's "green-cell type" category, but are not vanadocytes, gave positive Millon's and xanthoproteic reactions and he believed that their intracorpuscular material was composed of albuminous substances mixed with lipoids. Brien (1930) studied the same cells as Spek and found that the vacuoles stained brown with iodine-potassium iodide solution. He believed, because of this reaction, that they contained glycogen and, taking cognizance of Spek's results, stated, "ainsi, tout en considérant combien ces méthodes microchemiques sont approximatives, on pourrait admettre que la substance de la vacuole est formée de glycoprotéine". This was subsequently confirmed by Pérès (1948), who also used histochemical techniques.

The ferrocytes of *Pyura stolonifera* have now been shown to carry an aminopolysaccharide, as evidenced histochemically by the detection of polysaccharides and chemically by the release of reducing sugars on acid hydrolysis and the fact that hexosamine comprises a major part of these sugars. Since the ferrocytes stain metachromatically with toluidine blue, it would appear that the aminopolysaccharide is in the form of a sulphuric acid ester, possibly bound to protein. Presumably, the formation of the aminopolysaccharide occurs during the transition stage from "signet-ring" cells to morula-shaped cells, for stages subsequent to the signet-ring stage stain positively for polysaccharide. It will be recalled that these stages exhibit much activity in the form of cellular folding, cytoplasmic streaming, and vacuolar "bubbling". It is noteworthy, too, that the iron-containing material can be detected after the signet-ring stage. The association between the iron-containing material and the aminopolysaccharide may prove to be of more than passing interest.

The role of vanadocytes is not known. Winterstein (1909) has shown that the vanadium chromogen does not function as a respiratory pigment in a manner analogous to the haemoglobins. Henze (1912) suggested that it might function as a hydrogen acceptor but Webb (1939*b*) has shown that this is unlikely. Henze (1932) proposed that the chromogen might be concerned with the synthesis of tunicin and envisaged a process somewhat akin to photosynthesis because the CO_2 content of the plasma was less than that of sea-water. Florkin (1934), however, showed that the excess base of the plasma is much less than that of sea-water and hence the plasma does not take up any more CO_2 when equilibrated with sea-water.

George (1939) postulated that the cells of the green-cell type and other vacuolated cells acquire food molecules in the gut wall, subject them to enzymic activity, and pass them on to the tissues. In support he stated that histological sections reveal that the tissue spaces of the intestine are so arranged that the blood bathes directly the bases of the epithelial cells of the gut, to which the vacuolated cells are frequently attached. Other sections showed cells, mostly of the green-cell type, applied in large numbers to muscle tissue. The inference drawn was that a "large proportion of the blood cells serve as nutritive or nerve-cells for the tissues".

Although the ferrocytes of *Pyura stolonifera* occasionally can be found attached to various tissues, by far the greater number circulate freely in the blood or are lodged in the substance of the test. Moreover, the observations and experimental work recorded in this paper indicate that the role of the ferrocytes is that of synthesizing new compounds rather than the degradation of preformed compounds to provide nutrient materials for the tissues.

No function at present can be ascribed to the iron-containing material of *Pyura stolonifera* but it has been shown in this paper that this material is found in association with a polymerized amino sugar in the globules present in ferrocytes. That the material from these globules gives rise to the test substance of *Pyura stolonifera* will be shown in a subsequent paper.

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THE IMPORTANCE OF BACTERIA AND OTHER MICROORGANISMS IN THE SEA-WATER AT MACQUARIE ISLAND

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(*Manuscript received April* 5, 1954)

Summary

An account is given of some simple experiments on the decomposition of the giant kelp, *Durvillea antarctica* (Cham.) Hariot. Certain bacteria isolated from sea-water are listed and the marine origin of airborne bacteria at Macquarie I. is indicated. It is considered that, indirectly, kelp may form an important source of food for the seals and bird life of this region.

I. INTRODUCTION

The importance and complexity of the microbial populations of the seas are now well recognized. In reviewing the subject of marine microbiology, ZoBell (1946) has shown that bacteria, fungi, and yeasts are of particular significance in the decomposition of a wide range of plant and animal products under marine conditions. Prominent amongst these organic materials are the large brown seaweeds, one species of which, the giant kelp *Durvillea antarctica*, grows in great abundance within the narrow littoral zone at Macquarie I. Because of the heavy seas, the weed is continually being broken from the rocks and washed ashore in large quantities. Decomposition of this material is capable of supporting a variety of microorganisms and also releasing breakdown products, both of which can serve as nutrients for higher forms of life.

It is the purpose of this paper to indicate the role of microorganisms in this decomposition. The results were gathered by the author as biologist with the 1951-52 party of the Australian National Antarctic Research Expedition at Macquarie I.

II. METHODS

(*a*) *Collection of Bacteria from the Sea*

Plankton hauls were undertaken at several depths from the surface to 6 fm in both Hasselborough Bay and Buckles Bay whenever possible by J. D. Lindholm and the author. The surface water temperature was found to range from 5.7 to 7.5°C. Subsamples were taken from the collection bottle after each run and a small quantity inoculated into freshwater nutrient broth (Difco) immediately after returning to the island. After incubating at 25°C for several days, the resultant growth was streaked onto nutrient agar plates. Representative colonies were isolated and maintained for identification on return to Australia. No attempt was made to distinguish between truly marine bacteria and those introduced in drainage water from the soil. Although it is realized that the results may have been biased by the method of isolation, other circumstances prevented the execution of a more desirable procedure.

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(*b*) *Collection of Airborne Bacteria*

Plates of nutrient agar (Difco) were exposed to the air for 10 min at various elevations from sea-level to 1200 ft. After incubation at 30-32°C for 6 days, the colonies were counted and examined. From a knowledge of the wind speed, it was possible to make a rough estimate of the numbers of bacteria in aerial suspension under the conditions at the time of the experiment.

(*c*) *Kelp Decomposition*

A sample of healthy kelp, found to contain 1.6 per cent. total nitrogen, was taken from the rocks in Garden Cove together with a quantity of clean sea-water. The kelp was cut in pieces small enough to be contained in petri dishes, and exposed to the following treatments:

(1) Control: kelp and sea-water sterilized by autoclaving at 15 lb for 15 min.

(2) Kelp and sea-water not sterilized.

(3) Kelp and sea-water not sterilized; incubated at 25°C.

(4) Kelp sterilized externally with mercuric chloride (1:500), washed in successive batches of sterile water until residual mercuric chloride removed, and then placed in sterile sea-water.

(5) Kelp and sea-water both sterile; six kelp flies introduced.

(6) Kelp and sea-water both sterile; streaked with *Agrobacterium* sp. (from the sea-water).

(7) Kelp and sea-water both sterile; streaked with *Achromobacter* sp. (from the sea-water).

(8) Kelp and sea-water both sterile; streaked with *Bacterium* sp. (from the sea-water).

(9) Kelp and sea-water both sterile; streaked with *Alcaligenes* sp. (from the sea-water).

Each treatment was examined at intervals from January 4 until February 12, 1952. Except for No. 3, the dishes were all kept at room temperature (approx. 5°C) and exposed to the light (both normal and artificial). A fresh sample of kelp collected in March 1953 was analysed for total nitrogen content, using the normal Kjeldahl technique.

III. RESULTS

(*a*) *Heterotrophic Bacteria from Plankton Hauls*

The 22 cultures examined were found to represent the following genera (according to a key published by Skerman 1949): *Alcaligenes,* *Flavobacterium, Micrococcus, Agrobacterium, Achromobacter, Bacterium.* and *Bacillus.* Two lost their viability before identification was complete and others could not be given a satisfactory generic placing. Although the numbers of heterotrophic bacteria in the sea-water were not estimated, the diversity in the population is clear; a factor to be considered in relation to processes of decomposition.

(*b*) *Bacteria in Aerial Suspension*

These results are included in the present paper because they give some indication of the numbers of bacteria in the waters surrounding Macquarie I. Table 1 shows the numbers of bacteria per 100 cu. yd. of air at elevations from sea-level to over 1200 ft. Since the numbers show a striking decline with height above sea-level, it is apparent that they are marine in origin. Most were Gram-negative organisms, either rods or coccoid rods, the few colonies obtained at or above 200 ft being Gram-positive rods or micrococci. Although fungi were commonly found associated with decomposing kelp, no colonies developed on the plates with the exposure times used in this experiment.

TABLE 1

NUMBERS OF MICROORGANISMS IN AERIAL SUSPENSION AT MACQUARIE I.

Elevation Above Sea-level (ft)	Numbers of Bacteria per 100 cu. yd. Air
0	300
100	13
200	4
300	Nil
500	Nil
700	5
800	Nil
1000	Nil
1220	Nil

(*c*) *Decomposition of Kelp*

Since the observations made at the time of the experiment are in many respects repetitive, they have been condensed to emphasize the most important findings. An increase in temperature from 5 to 25°C caused a marked stimulation of the microflora. After only 2 days at 25°C, bacterial colonies had developed and the kelp was beginning to brown. The parallel treatment at 5°C did not show similar signs until 7 days later, by which time the incubated kelp was in an advanced stage of decomposition and covered with a heavy microbial slime. In every treatment, bacterial development was almost entirely restricted to the parts of the kelp above water and to the surface of the water itself.

Although microbial growth was stimulated by raising the temperature, this cannot be taken to indicate that only microorganisms with a relatively high optimum temperature range are concerned in the decomposition of kelp under sub-antarctic conditions. It is probable that the various components of the microflora are adapted for growth and activity at low temperatures. It is also probable that truly psychrophilic microorganisms might be present in the sea-water, although these could not be demonstrated from examination of bacteria from the soils of Macquarie I. which are exposed to similar temperatures (Bunt and Rovira 1954).

Where kelp flies had been introduced, activity was only slightly slower than at 25°C, thus indicating the highly important role of these insects in the decomposition process and their ability to offset the effects of low temperature on microbial activity. The exact function of the flies is not certain. They probably act merely by spreading active inocula over the algal material, thus eliminating the period that would otherwise be required to build up an effective bacterial population. Kelp fly larvae were not used in the experiment. Their importance will be discussed later.

The kelp that had been surface-sterilized showed no signs of decomposition after 5 wk other than a browning and deflation of the tissues. No bacteria appeared to be present. Subsequent inoculation with unsterile sea-water caused decomposition. The culture of *Achromobacter* sp. showed visible growth on the kelp surface after 3 days and the other isolates could be seen in 4 days. After 5 wk, however, these bacteria had caused little or no visible change in the kelp, despite their good growth. This points to the complexity of the breakdown process which in none of the treatments, all well-aerated, wholly resembled decay in the field, a process typified by a sharp, penetrating, unpleasant odour and, in stagnant water, abundant sulphide production, indicating anaerobic conditions.

In the unsterile treatments (with and without kelp flies), a wide range of microorganisms was observed. The bacteria all appeared to be Gram-negative but varied considerably in morphology. Penicillia were prominent and several types were found which do not appear to be soil forms in the light of other investigations by the author (unpublished data). Yeasts and protozoa were present in very large numbers, the yeasts being prominent within the kelp tissues while the protozoa seemed mostly to be situated in the liquid surrounding the kelp. This would be expected since the yeasts are concerned with the breakdown of carbohydrates in the tissues whilst the protozoa are largely bacterial feeders.

IV. DISCUSSION

The decomposition of kelp may be quite rapid under suitable conditions. Several distinct decay situations are recognizable. Probably the most important is on the open beaches and between the rocks just above high tide where the drainage is relatively free. On the beaches, extensive banks of dead kelp may be seen partly mixed with the beach sediments and just out of reach of normal seas. Amongst the rocks the dead fronds often form deep tangled masses. Both situations are favoured as hauling-out areas by seals so that the material is crushed to some extent by their movements and also fouled by their excrement, thus favouring microbial activity. Here too, the kelp fly is most important, principally in the larval stage, for it occurs in very great numbers and is apparently nourished by the rotting seaweed and the masses of microbial slime associated with the kelp. Unfortunately, the author's laboratory observations were limited to the adult stage as the 1951-52 expedition was relieved before the study could be extended. Once decomposition begins, the kelp soon becomes converted into a foul-smelling semi-liquid mass. As the kelp fly pupates on the sand beneath the kelp and on partly decomposed fronds, it is probably only active in the early stages of decay before the material becomes wet, compacted, and badly aerated.

Stagnant salt-water rock pools also serve as accumulation pockets for the dead kelp. Under these conditions, the kelp fly does not appear to be important and decomposition is entirely microbial, the material becoming blackened owing to sulphide production, and the water opaque and yellow. From all these situations, the decomposed seaweed eventually washes back into the sea.

In the wet tussock grassland around the coast, "poa bogs" are common. They occur in badly drained peaty areas and consist of sink-holes (usually 3-4 ft wide and several feet deep filled with water or mud) which lie between the large tussocks of *Poa foliosa* Hook. Kelp is blown into such areas in small quantities and must exert some effect on the chemical status of the soil. However, it may safely be assumed that the marine life in the vicinity of Macquarie I. receives most of the benefit from the kelp food source.

It is clear that there is both the scope and the necessity for more detailed investigations into this aspect of sub-antarctic marine ecology. At present, the importance of kelp compared with plankton as a primary source of food for higher animals in the vicinity of Macquarie I. is not known. An estimate of the total quantity of kelp washed ashore per annum would be most valuable as it would indicate the food potential of this material and provide some measure of its effect on the productivity of the surrounding sea.

If most of the nutrients released from the kelp were ultimately utilized by marine animals, e.g. fish, restricted in distribution to coastal waters and edible to birds and mammals, then it may be possible to show that kelp assists, not only in the nutrition of the strictly marine fauna, but also in the sustenance of the large populations of seals, penguins, and birds of flight that visit Macquarie I. during the breeding season.

V. ACKNOWLEDGMENT

The author wishes to thank the University of Sydney for making laboratory facilities available in the Faculty of Agriculture during the completion of this report.

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THE CHAINOMATIC PYCNOMETER: AN INSTRUMENT FOR THE RAPID DETERMINATION OF THE SALINITY OF SEA-WATER

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Summary

The Division of Fisheries, C.S.I.R.O., has modified the chainomatic pycnometer of Pettersson and Pettersson (1929) for use as a self-contained field unit for the determination of Cl‰ to a minimum accuracy of ± 0.075.

I. INTRODUCTION

As early as 1890 Krummel had investigated the possibility of direct determination of the specific gravity of sea-water, by the use of hydrometers of conventional pattern. Later Nansen, in 1900, also used hydrometers for the determination of the specific gravity and the salinity of sea-water. However, Nansen was quick to realize the limitations of a hydrometer with an emergent stem, and tried to improve the pycnometric methods by using totally immersed floats and holding them in equipoise with added weights. Pettersson and Pettersson (1929) greatly improved on the original idea of Nansen by using a gold chain as the weight source and by other mechanical improvements. They described two pycnometers, one with the gold chain as a tail on the float and operated in a tall cylinder in some 500 ml of sea-water, and the other utilizing the chainomatic principle in which gold chain was added link by link from a drum to the top of the float. This second instrument was essentially a laboratory instrument and according to Pettersson and Pettersson, if the temperature was controlled and accurately known, capable of high accuracy in density determination.

The Division of Fisheries, C.S.I.R.O., has been making extensive investigations of the coastal and estuarine environments of Australia and a rapid accurate method of Cl‰ determination which could be used by field staff under the varying and often primitive conditions of field operation seemed highly desirable. The pycnometric method of Cl‰ determination by measurement of density and temperature simultaneously was finally chosen because it is a direct physical method which, without the range of equipment needed for a chemical determination or the skill and somewhat higher expense required to construct and maintain electronic equipment, is in our experience capable of high accuracy in the hands of semi-skilled operators. Moreover, it is capable of continuous linear operation over the whole range of chlorinity from sea-water to fresh water.

The Pettersson chainomatic pycnometer was adapted to our needs and the model now in use by the Division of Fisheries departs in the following manner from the original design:

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(i) It is essentially a field unit of light weight and folds completely into a wooden carrying case 15 by 7½ by 3½ in.

(ii) The glass parts are extremely rugged.

(iii) Certain mechanical features, particularly the tension clutch (7, Fig. 3) and the "Perspex" chain guide (10, Fig. 3), have been designed to ensure perfect reproducibility of chain setting by maintenance of constant tension on the surplus chain on the chain roller.

(iv) The calibration is in Cl‰ units and calibration graphs enable rapid conversion of instrument data into Cl‰.

The chainomatic pycnometer used by the Division of Fisheries, C.S.I.R.O., was exhibited at the Eighth Pacific Science Congress at Manila in November 1953,* and attracted much interest from the oceanographers there. As a result of this interest a sample unit was sent to Canada for trial use in coastal oceanographical studies, and immediate steps were taken to finalize certain technical improvements to the design and to publish a description of its design and operation.

II. DESCRIPTION

In the design of the chainomatic pycnometer certain desirable features had to be considered.

(i) The whole unit should be small, compact, and of light weight; yet suitable for transport in all the rough conditions of field operations in the estuarine programme of the Division of Fisheries.

(ii) The instrument should require a water sample of between 75 and 100 ml, but no more, for operation.

(iii) It should determine Cl‰ with an accuracy of ±0.05 over a range of 0-20‰.

(iv) It should be mechanically simple so that field maintenance can be carried out.

These desiderata are to some extent self-contradictory, but by trial and error and much critical field use, a chainomatic pycnometer was finally evolved in which they were all incorporated.

Figure 1 shows the unit being lifted out of its carrying case, the box board upon which the instrument is mounted being hinged at the lower end. When the box board is raised to the vertical it is locked into the position shown in Figure 2 by a spring clip. The pycnometer is then set up for operation as described in Section III, and Figure 3 shows the arrangement of parts from the front view.

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* Subsequent to the Manila Congress, an offer has been received from the G. & M. Manufacturing Company, New York, U.S.A., to manufacture the instrument for general oceanographical use, and any enquiries regarding its supply should be directed to this firm.

The float of thick-walled Pyrex glass (11, Fig. 3) is blown with a convex top to hold the chain and is tapered to bring the mercury to the centre of the base so that the combined centre of gravity of the float and of the mercury is as low as possible. The float, 32 mm in diameter and 5 cm long, is carefully weighted with mercury so as to just float at 35°C in distilled water. (The float for instrument No. 9 is 28.274 g in weight and has a volume of 28.722 c.c. at 15°C.) A reference line is scribed around the middle of the float and filled with coloured glass ink.

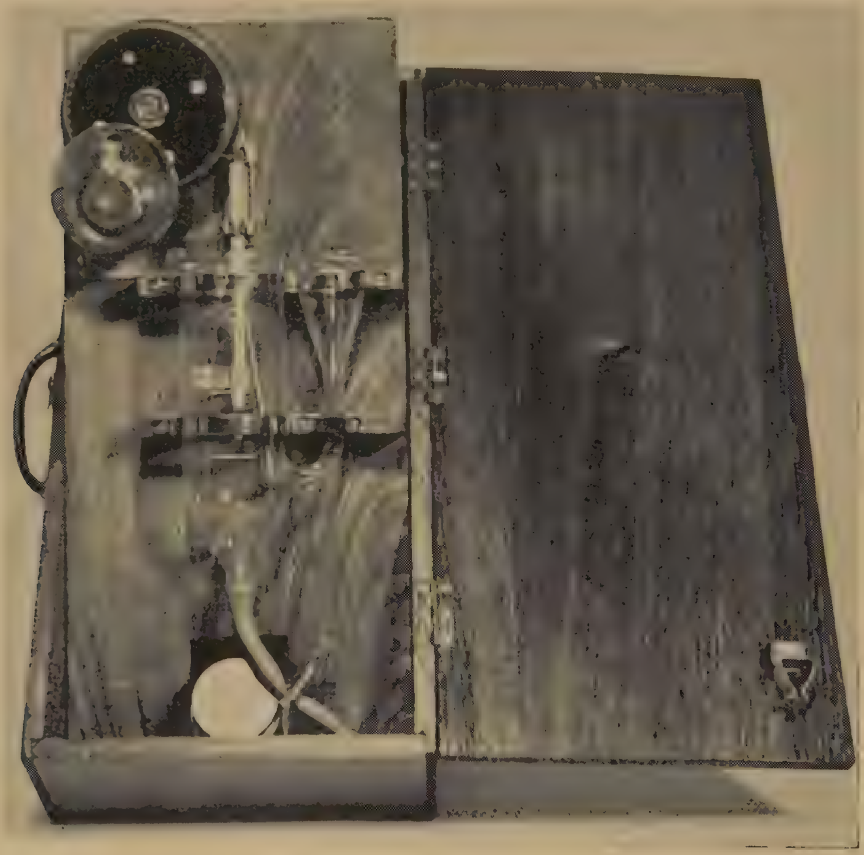

Fig. 1.—Pycnometer with base board half lifted out of its cover. The chain tension clutch is not fitted.

The float is contained in a float chamber (3, Fig. 3) fitted with a side funnel to facilitate filling with the sample. The base of the float chamber is tapered to a drainage tube closed by a screw clamp. At its base indentations are blown in the glass so that when the sample is being drained out the float cannot constrict the opening. Two reference lines are scribed on the float chamber, the lower being equipoise setting for the float and the other a level mark for the height of water.

The thermometer (8) is held by clips to the baseboard. It is calibrated from 0 to 40°C in 1° intervals. To its lower end a "Perspex" chain guide (10) is fastened at a height just below the water level. This prevents the float rising above water-level prior to the additions of chain. The chain passes through a diabolo-shaped opening and any cross links are either straightened or arrested by this guide. The gold chain is of 18 ct gold 2 mm link trace chain and is anchored to the "Perspex" drum (6) of 7.5 cm diameter. A flat bottom helical groove carries the chain and prevents any variation in its distribution on the drum.

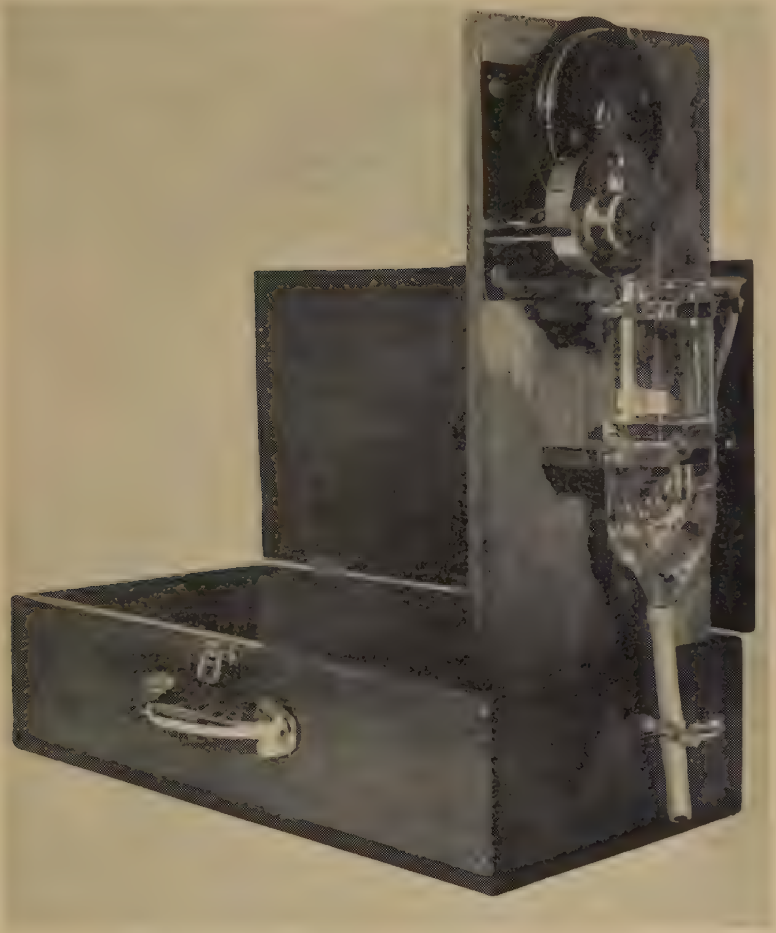

Fig. 2.—Side view of pycnometer set up for routine determination. The chain tension clutch is not fitted.

This drum is riveted to a spur gear wheel and mounted on an axle fastened to the baseboard. The spur wheel in turn is geared to a smaller spur gear fitted to the main shaft. Two dials indicate the length of chain wound from the drum onto the top of the float. The primary dial (5) is fitted to the main shaft and is calibrated into 10 units numbered 0-9, each of which is subdivided into quarters; a total of 40 calibration marks is

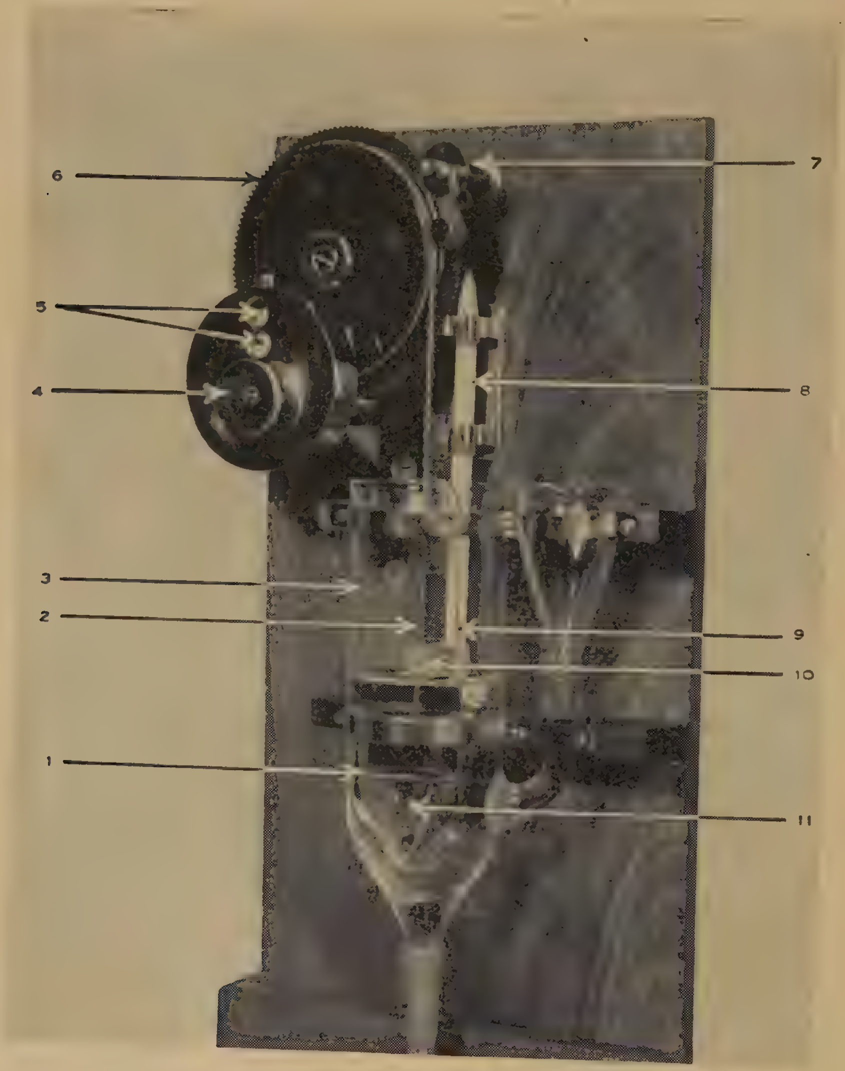

Fig. 3.—Front view of working parts of pycnometer. 1, reference lines; 2, gold chain; 3, float chamber; 4, chain adjusting knob; 5, chain setting dials; 6, chain drum; 7, tension clutch; 8, thermometer; 9, float lifter; 10, chain guide; 11, float.

thus available. The secondary dial (5) is actuated by a single tooth on the primary dial and moves one unit for each complete revolution of the primary dial. This dial is calibrated in 20 units, numbered 1 to 20.

A tension clutch (7), actuated by the main spur gear wheel, exerts a constant tension on the gold chain as it is wound back onto the drum. On the opposite movement of the drum the tension pad is thrown off contact with the drum and the chain falls freely under its own weight.

Lying under the float chamber is a wire float lifter (9). This is used to lower the float into or remove it from the float chamber during the setting up or dismantling of the instrument. Also if air bubbles form on the outside of the float, these can be easily removed by lifting the float out of the water and gently lowering it back again.

For field operation it has been found convenient to fit a screw attachment to the box of the unit which can be fastened to an ordinary heavy photographic tripod. The tripod can then be set up anywhere and adjusted to give a horizontal setting for the base of the chainomatic pycnometer.

III. OPERATION

The instrument is lifted out of its carrying case and clipped into a vertical position against the lid. Some care should be taken to ensure that the instrument is on a level base or that the tripod is properly adjusted. The chamber is filled with distilled water to the level mark and a small quantity of detergent added. With the chain guide turned aside by twisting the thermometer, the float is lowered into the chamber by means of the wire float lifter. The gold chain is lowered to the level of the guide, which is then twisted back into position such that the chain lies directly in line with the hole in the guide. The chain is completely unwound onto the float, which is then gently agitated with the float lifter to enable the detergent to thoroughly wash the float and chain. Care should be taken to ensure the complete removal of air bubbles from the chain and float, a slender glass rod being used if necessary. The instrument is then drained and flushed twice with distilled water.

The chamber, float, and chain are flushed with the sample to be analysed. With the chain fully unwound, sufficient of the sample is added to cover the float. This flushing is then drained off and the chamber filled to the level mark with the sample. The chain is carefully wound back onto the drum, care being taken that when any cross linkages occur in the chain they are removed before they reach the chain guide. If this is not done, the chain may be seriously distorted or stretched in being forced through the guide, necessitating a lengthy recalibration of the instrument. As soon as the float becomes buoyant, it should be inspected to ensure that it floats approximately level, and if not, the chain should be redistributed on it with the glass rod until it does. Also, it is necessary to ensure that there is no obvious building up of the chain on the float into unnecessary clumps. The chain is then carefully raised until the reference line on the float is exactly level with that on the float chamber. The dials are read to 0.01 and the temperature to 0.1°C. The chain is unwound again until the float is no longer buoyant and then carefully raised to equipoise and the dials once more read. The two readings should agree to within less than 0.05 and should be repeated if they do not. All readings must be taken by *raising* the float to the calibration mark, as the chain tensor is only effective in the ascending motion. Care should be taken to ensure that there are no cross links in the chain between the float and the chain guide before each reading.

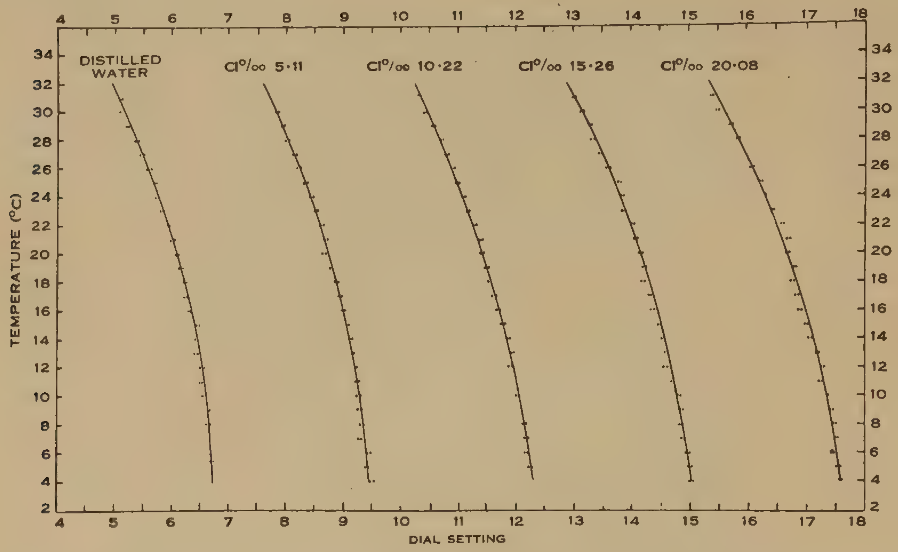

Fig. 4.—Relationship between dial setting and temperature for distilled water and waters of Cl‰ 5.11, 10.22, 15.26, and 20.08, using instrument No. 9. Duplicate values at each reading are given.

When one determination is complete, the chain is once more unwound onto the float and the instrument drained. There is no need to flush the instrument with distilled water between samples. It is more effective to flush only with the next sample to be determined.

The chlorinity of the sample is determined by application of the mean dial reading and temperature to the calibration chart of the instrument (Fig. 5).

IV. Calibration

Pettersson and Pettersson (1929) give a formula by which the specific gravity of a sample can be computed if certain weight-volume characteristics of the float and the links of the gold chain are known. From the specific gravity at the temperature of determination the σ_0 value can be calculated. Knudsen's (1931) tables can then be used to calculate the Cl‰ or S‰ equivalent of the σ_0 value. Since our interest in the chainomatic pycnometer was in its application to Cl‰ determination, we have calibrated it directly in Cl‰ units.

A series of Cl‰ standards was prepared by diluting local sea-water with distilled water, and the Cl‰ values of these standards were carefully determined by Knudsen titration. Two samples of each standard were then taken, one being warmed to 40°C, the other cooled to about 3-4°C.

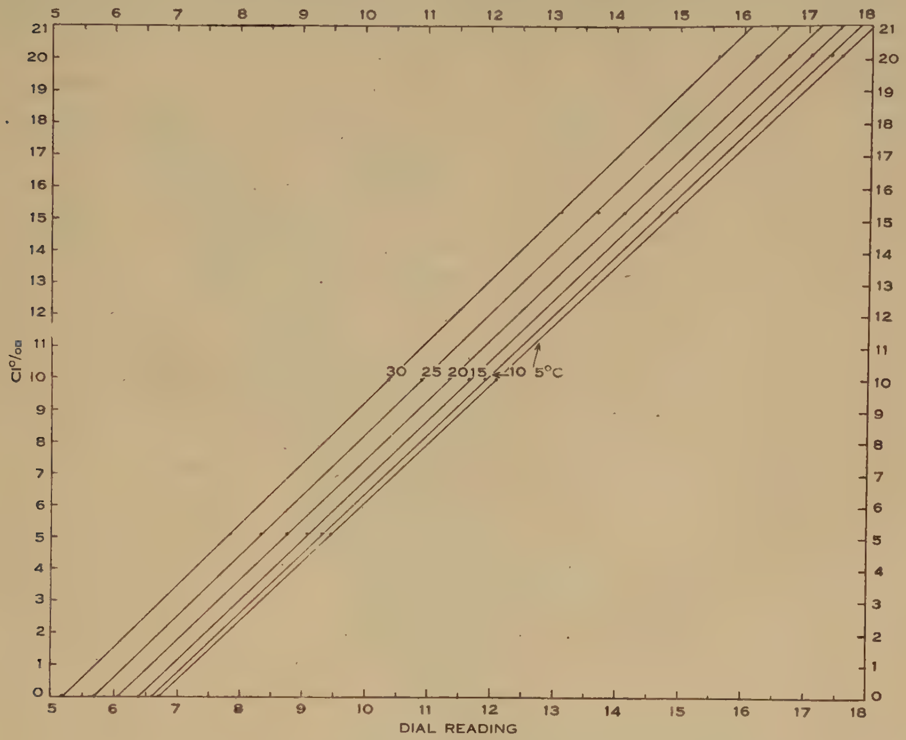

Fig. 5.—Calibration graph of instrument No. 9 for Cl‰ range 0 to 21, and for temperature range 5-30°C in 5° intervals.

The warmed sample of each standard was poured into the chainomatic pycnometer and the float balance ascertained. The initial readings were probably in error because sufficient time had not been allowed for equilibration between the float and water temperatures. For this reason the equipoise settings above 30°C are not considered very reliable, and the calibration has not been extended above this temperature. As the water temperature fell equipoise readings were taken at about 1°C apart.

After this standard water had cooled to near room temperature it was drained off and the cooled sample of the same Cl‰ value added. The chain settings at about each 1°C rise in temperature of this standard water were read, until it had reached room temperature. The temperatures, chain, and setting values were then plotted against one another over a temperature range of 5-30°C. A smooth curve was drawn through the data.

The process was repeated for each of the Cl‰ standard waters.

The complete series of such plottings from which the calibration curves were drawn for pycnometer No. 9 are shown in Figure 4.

From these curves, the dial settings corresponding to temperatures of 5, 10, 15, 20, 25, and 30°C were read for each of the Cl‰ values and a graph of the relationship between Cl‰ and dial setting at each of these temperatures was constructed (Fig. 5). It is evident from the figure that a linear relationship exists between Cl‰ and dial setting at constant temperature. Such a calibration graph is useful for field interpretation of instrumental data, but for fullest accuracy of interpretation it is necessary to construct calibration graphs with a smaller Cl‰ range and with 1°C temperature intervals. Such a graph for instrument No. 8 is shown in Figure 6.

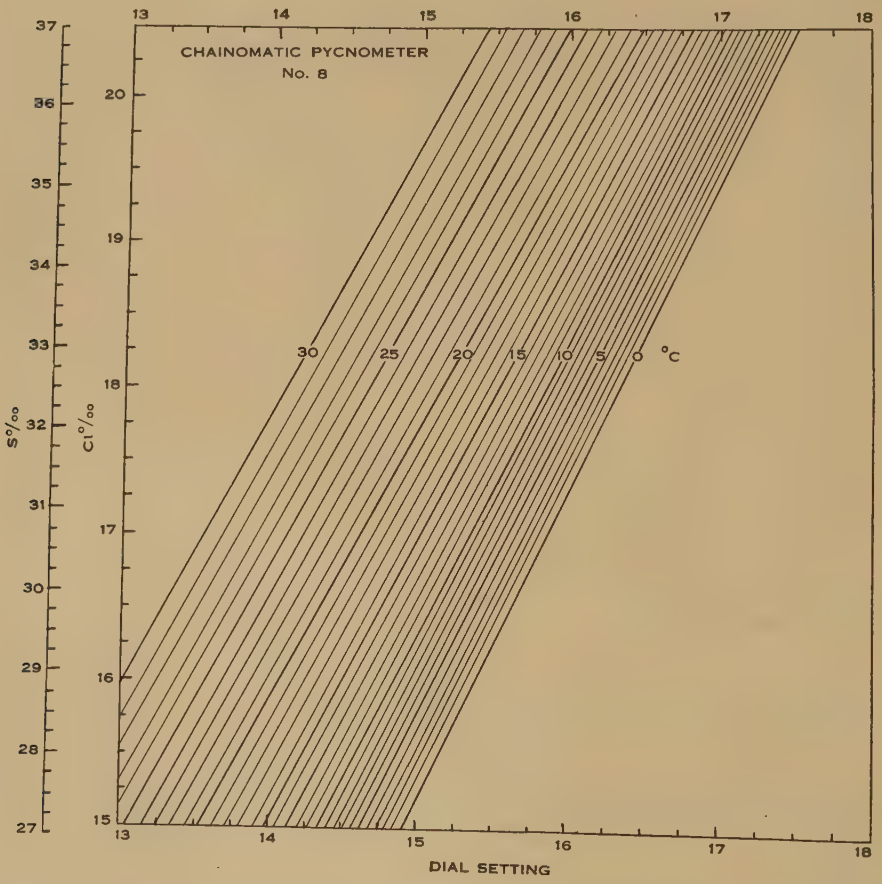

Fig. 6.—Calibration graph of instrument No. 8 for Cl‰ range 15-20, and for temperature range 0-30°C in 1° intervals.

The accuracy with which a chainomatic pycnometer can determine the Cl‰ of a sample is mainly dependent upon the ability of the dials to give an exact and reproducible measure of the length of chain resting on the float at equipoise. In order to achieve this, three points have to be watched: (i) that each time the chain is wound onto the drum the revolution of the drum will take up the same length of chain; (ii) that the chain lies with a reproducible tension around the drum when reading at equipoise; (iii) that there are no cross linkages in the whole length of chain not lying on the float. Any of the above three factors could cause falsely high dial readings at equipoise by apparently shortening the chain above the float. The first is effected by the helical groove drum (6, Fig. 3) which prevents the haphazard piling up of the chain on itself as it is wound onto the drum, in effect altering the diameter of the drum and thus the drum revolution to chain length ratio. The second is achieved by the clutch-tensor (7, Fig. 3), which prevents and removes any slackness of the chain lying on the drums. This is designed to be thrown out of action when the chain is being unwound, otherwise it would then cause a slackening of the chain on the drum. The third factor of chain cross linkages would be ideally avoided by the use of perfect circle links in the chain. However, these have not been procurable as yet. The use of the diabolo-shaped aperture (10, Fig. 3) in the chain guide serves as a watchdog, and will remove the cross linkages. These must nevertheless be carefully watched, as they can jam the chain and cause serious distortions in the chain length by stretching sections of it. Moreover, the chain guide does not prevent cross linkages occurring between it and the float, which must be manually removed before reading the dial.

V. ACCURACY

In order to test the sheer mechanical accuracy of the instrument, four operators of varying degrees of knowledge of the instrument were given a series of unknown Cl‰ standards to determine with the chainomatic pycnometer. The only instructions given were those in Section III of this paper.

Each was then asked to determine Cl‰ values in a predetermined order of descending values and then to repeat the series, in any order. The results of these tests are given in Table 1.

It is evident that in most tests the operator in the second determination on the same Cl‰ (columns 3 and 4) has learnt to use the instrument more efficiently and has obtained better accuracy than on the first (columns 1 and 2). However, taking all readings into account there seems ample justification for claiming that the chainomatic pycnometer as used by the Division of Fisheries, C.S.I.R.O., can under all circumstances determine Cl‰ to within ±0.075 Cl‰ units; and in the hands of trained operators can approach ±0.05 units.

As such accuracy is sufficient for our purposes we have not endeavoured to read temperatures to better than 0.1°C, although at

TABLE 1

CHLORINITY DETERMINATIONS (‰) BY DIFFERENT OPERATORS

Operator	By Titration (standard)	By Pycnometer No. 9				Mean Error
		1	2	3	4	
J.T.	20.28	20.40 +0.12	20.40 +0.12	20.25 −0.03	20.26 −0.02	0.07
G.K.	20.28	20.40 +0.12	20.25 −0.03	20.38 +0.10	20.39 +0.11	0.09
D.T.	20.26	20.20 −0.06	20.20 −0.06			0.06
H.J.	20.10	20.15 +0.05	20.18 +0.08	20.10 0.00	20.10 0.00	0.03
G.K.	16.12	16.15 +0.03	16.10 −0.02	16.21 +0.09	16.13 +0.01	0.04
H.J.	15.26	15.31 +0.05	15.32 +0.06	15.32 +0.06	15.32 +0.06	0.06
J.T.	14.91	14.90 −0.01	14.91 0.00			0.01
D.T.	12.84	12.80 −0.04	12.85 +0.01			0.03
G.K.	11.96	12.03 +0.07	12.02 +0.06	12.00 +0.04	12.00 +0.04	0.05
D.T.	11.29	11.20 −0.09	11.25 −0.04			0.07
J.T.	10.53	10.57 +0.04	10.58 +0.05	10.45 −0.08	10.45 −0.08	0.06
H.J.	10.22	10.22 0.00	10.21 −0.01	10.19 −0.03	10.21 −0.01	0.02
J.T.	8.43	8.45 +0.02	8.44 +0.01	8.48 +0.05	8.44 +0.01	0.02
G.K.	8.30	8.33 +0.03	8.33 +0.03	8.35 +0.05	8.36 +0.06	0.05
D.T.	7.92	7.91 −0.01	7.93 +0.01			0.01
J.T.	5.69	5.57 −0.12				0.12
D.T.	5.29	5.25 −0.04	5.27 −0.02			0.03
H.J.	5.11	5.17 +0.06	5.15 +0.04	5.10 −0.01	5.15 +0.04	0.04
G.K.	4.28	4.25 −0.03	4.30 +0.02	4.32 +0.04	4.33 +0.05	0.04
						0.05

temperatures above 15°C it is evident from Figure 6 that higher accuracy in temperature determination could increase the accuracy of results.

Pettersson and Pettersson (1929) claim an accuracy of ±0.00002 units in specific gravity, corresponding to a chlorinity difference of ±0.02 at constant temperature; and it is evident from our design, in which despite lack of temperature control or accuracy of reading, accuracies of ±0.05 Cl‰ are obtained, that these results could be obtained with their laboratory instrument.

Moreover, with certain improvements in chain detail and the type of float, we are confident that our instrument could be made mechanically more reliable with increase in accuracy of Cl‰ determination, without sacrificing the field portability, ruggedness, and simplicity of the present design.

However, as the instrument as it stands is satisfactory for determination of Cl‰ in the present coastal and estuarine studies it is possible that such improvements will only be made if the improved instrument has more general applications in oceanography.

VI. Discussion

(*a*) *Distortion of Chain*

In using the chainomatic pycnometer two sources of calibration error with time have been found. The first error is due to corrosion of the gold chain. The original gold chain fitted to the pycnometer was ordinary commercial chain of 11 ct. After some period of field work the calibration of the instrument was found to be incorrect. Examination showed that corrosion at the weld on each link of the chain had occurred, and this naturally altered the calibration. This was rectified by the use of heavier plated 18 ct chain on the next model.

A more serious source of error was found to be due to elongation of the gold chain by careless operation. As each link of the gold chain passes through the chain guide, a cross link may occasionally jam in the aperture. When this happens, if the operator is careless, the chain above the chain guide will be stretched. The original calibration will then be in error and unless the elongation of the chain is uniform over its whole length, a variable departure from the original calibration will not allow of the calculation of a simple error table. Once the elongation has introduced significant errors into the original calibration graphs a recalibration will be necessary. Extreme care should therefore be taken to guard against this source of error. Occasional testing of the instrument against a standard water of known Cl‰ is an excellent check on the possibility of this fault having developed.

(*b*) *Variable Piling up of Gold Chain*

The increasing scatter of the data around the mean curve, with increase in chlorinity, exhibited in Figure 4 is due in large measure to variations in the height of the pile of gold chain on the top of the float. This leads to a variation in the length of chain suspended from the drum to the top of the float, for a constant combined weight of chain and float, and gives different dial settings for a solution of the same density at constant temperature. A study of the reproducibility of dial settings giving fixed weights of chain was made by directly weighing a dummy float with increasing amounts of chain resting in the recess, using exactly similar chain, drum, dials, etc. to those used in the pycnometer. It was found that the reproducibility of dial settings decreased with increasing chain weight at a very similar rate to the accuracy of the chlorinity determinations with increasing chlorinity. This decreasing reproducibility was found to be due to the haphazard piling up of the chain in the float recess, which became less reproducible as the quantity of chain increased. These findings suggest that for more accurate work at higher chlorinities it would be advisable to construct a float of greater density to be used with the same instrument but using much less chain to cover a limited chlorinity range of 16-20 for example. Another possible method of overcoming this increasing inaccuracy would be to introduce a shaped cone recess into the float instead of its present simple dish recess. For the purposes for which the instrument was developed, these improvements were not considered necessary.

(*c*) *Determination of Relative Density by the Pycnometer*

While the pycnometer has been directly calibrated in Cl‰ units determined by Knudsen titrations, it is basically measuring the density of the samples. In view of this, consideration has been given to the possibility of correlating the dial readings obtained for solutions of particular Cl‰ values with the relative densities of the solutions as given by Knudsen's (1931) hydrographic tables.

Assuming that the instrument is measuring the density of a solution, it can be postulated that

$$\sigma = A . DR + B, \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (1)$$

where σ = density of the solution at a particular temperature,
DR = dial reading at equipoise,
A, B = empirical constants characteristic of the particular instrument.

The empirical constants A and B were determined for pycnometer No. 9 by substituting in the following equations, derived from (1) above, Knudsen's densities at 15°C for solutions of Cl‰ 5.11, 10.22, 15.26, and 20.08, and the corresponding dial readings from the graph in Figure 4 at 15°C.

$$A = (\sigma_1 - \sigma_2)/(DR_1 - DR_2), \quad \ldots\ldots\ldots\ldots\ldots \quad (2)$$
$$= 0.0025993 \text{ for pycnometer No. 9.}$$

$$B = (DR_1\sigma_2 - DR_2\sigma_1)/(DR_1 - DR_2), \ldots\ldots\ldots \quad (3)$$
$$= 0.98266 \text{ for pycnometer No. 9.}$$

Equation (1) becomes

$$\sigma = 0.0025993DR + 0.98266. \ldots\ldots\ldots\ldots \quad (4)$$

If the dial readings for a particular Cl‰ value at temperatures above and below 15°C are read from the graphs in Figure 4 and substituted in (4), the curves for calculated densities shown as broken lines in Figure 7 are obtained. Comparison of these calculated densities with those plotted from Knudsen's tables, shown as unbroken lines in Figure 7, show that

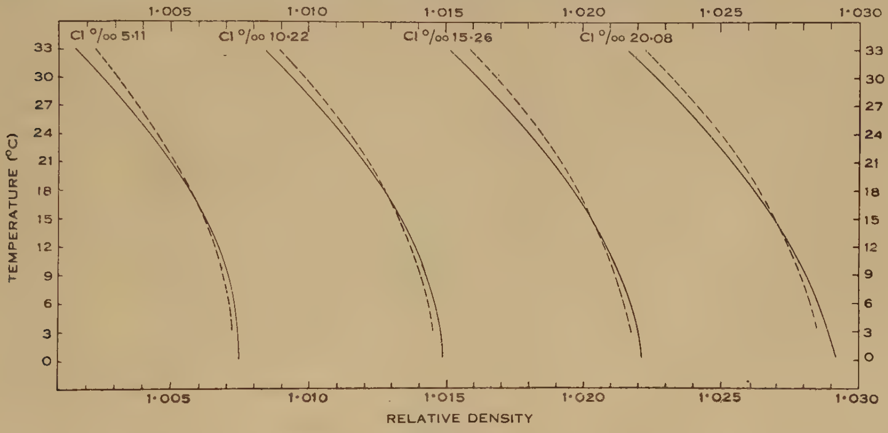

Fig. 7.—Relationship between relative density and temperature of waters of Cl‰ 5.11, 10.22, 15.26, and 20.08 (solid lines) according to Knudsen's table and the calculated densities using the data in Table 2 (broken lines).

while the two densities coincide quite well at 15°C, the temperature at which constants A and B were determined, there is an increasing discrepancy with temperature difference. In order to account for this discrepancy a correction was made to the calculated densities to allow for volume changes in the float with temperature, using the equation

$$V_t = V_{15} + \gamma V_{15}(t - t_{15}), \ldots\ldots\ldots\ldots \quad (5)$$

where V_t = volume of float at t°C,

V_{15} = volume of float at 15°C,

γ = coefficient of cubic expansion of the float (taken as solid glass).

Thus

$$\text{corrected density} = \text{calculated density} \times (V_{15}/V_t). \ldots. \quad (6)$$

Table 2 shows the effect of this correction, the calculated density error, Δ, giving the difference between calculated density and Knudsen's density, and the corrected density error, Δ', the difference between the corrected density and Knudsen's density. It will be seen that the Δ′ values are all much less than the Δ values at all temperatures and densities.

The use of an equation of the form

$$\sigma' = \text{corrected density} = (V_{15}/V_t)\,(A \,.\, DR + B) \;\ldots\ldots\; (7)$$

could therefore be used to transform dial readings of an instrument calibrated directly in Cl‰ units into specific gravity equivalents with an accuracy of ±0.0001.

TABLE 2

RELATIVE DENSITY DETERMINATIONS (PYCNOMETER NO. 9)

Volume of float at 15°C, 28.7222 c.c.; at other temperatures, calculated from (5). Coefficient of cubic expansion of float, 0.25×10^{-4}

Chlorinity (‰)	Temp. (°C)	Knudsen's Density	Dial Reading (*DR*)	Calc. Density σ*	Calc. Density Error Δ†	Corrected Density σ′‡	Corrected Density Error Δ′§
5.11	6	1.00723	9.41	1.00712	+0.00011	1.00735	−0.00012
	15	1.00627	9.07	1.00624	+0.00003	1.00624	+0.00003
	24	1.00432	8.43	1.00457	−0.00025	1.00434	−0.00002
	30	1.00259	7.86	1.00309	−0.00050	1.00271	−0.00012
10.22	6	1.01458	12.20	1.01437	+0.00021	1.01460	−0.00002
	15	1.01333	11.77	1.01325	+0.00008	1.01325	+0.00008
	24	1.01123	11.10	1.01151	−0.00028	1.01128	−0.00005
	30	1.00944	10.47	1.00987	−0.00043	1.00949	−0.00005
15.26	6	1.02172	14.94	1.02149	+0.00023	1.02172	0.00000
	15	1.02029	14.49	1.02032	−0.00003	1.02032	−0.00003
	24	1.01807	13.81	1.01856	−0.00049	1.01833	−0.00026
	30	1.01620	13.15	1.01684	−0.00064	1.01646	−0.00026
20.08	6	1.02858	17.54	1.02825	+0.00033	1.02848	+0.00010
	15	1.02697	17.05	1.02698	−0.00001	1.02698	−0.00001
	24	1.02461	16.30	1.02503	−0.00042	1.02480	−0.00019
	30	1.02270	15.62	1.02326	−0.00056	1.02288	−0.00018

* Obtained from equation (1); (4) for pycnometer No. 9.
† Knudsen's density —σ.
‡ Obtained from (6).
§ Knudsen's density —σ′.

However, if the fullest accuracy in the determination of specific gravity by this instrument were desired then either a calibration against solutions of known specific gravity or the use of a float made of material of low thermal expansion such as silica as recommended by Pettersson and Pettersson (1929) should be used.

VII. CONCLUSIONS

This chainomatic pycnometer has been found to be a robust and reliable instrument capable of determining chlorinities with an accuracy of ±0.05 Cl‰ units over the whole range of Cl‰ from 0.0 to 20.0. It is suitable for use as a field instrument and can be operated efficiently by semi-skilled personnel. In its present form its chief use would be for rapid on-the-spot chlorinity determinations in estuarine studies, though it can be useful in coastal studies where an accuracy of ±0.05 is sufficient. If used with reasonable care it requires very little servicing, though its calibration must be checked periodically. Suggestions have been made for increasing the accuracy of the instrument, and the authors feel confident that with improved thermometers, chains, and floats an accuracy of ±0.01 Cl‰ units could be quite easily achieved, certainly in restricted chlorinity ranges.

An empirical equation has been derived for the determination of relative densities of samples from dial readings and temperatures with an accuracy of approximately ±0.0001. The equation is useful for rough density determinations. However, if greater accuracy is required, it is necessary to calibrate the pycnometer in density units instead of chlorinity.

VIII. ACKNOWLEDGMENTS

Thanks are extended to members of the staff of the Division of Fisheries, C.S.I.R.O., who have used the instrument and offered valuable criticism, and particularly for the patient help of the workshop staff, who have been responsible for the engineering design and production of the instrument.

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AUSTRALIAN SIPUNCULOIDEA

I. THE GENERA SIPUNCULUS, XENOSIPHON, AND SIPHONOSOMA

By S. J. Edmonds*

(*Manuscript received August 23, 1954*)

Summary

This paper deals with the Australian sipunculids of the genera *Sipunculus*, *Xenosiphon*, and *Siphonosoma*. *Sipunculus angasi* Baird, 1868, a species allied to *S. nudus* and *S. robustus*, is redescribed from south, south-eastern, and eastern Australia. A sipunculid from New South Wales is redescribed and assigned to the genus *Xenosiphon*. *Siphonosoma cumanense* (Keferstein 1867) and *Siphonosoma vastum* (Sel. and Bül. 1883) are redescribed from Queensland and Western Australia.

I. Introduction

Although they are frequently found along the Australian coast, sipunculids have received little attention from workers in this country. The present series of papers, based on the study of specimens obtained mostly from the State Museums and Universities, aims to bring up to date as far as is possible the knowledge of the known Australian forms. This paper deals with the genera *Sipunculus*, *Siphonosoma*, and *Xenosiphon*; the other genera will be discussed and a key to the Australian forms given in a subsequent paper. Species recorded by previous workers but not found amongst the specimens examined by the present writer will only be listed. As many parts of the coastline have not yet been carefully explored by collectors the forms mentioned in the present papers probably do not represent the total sipunculid fauna of the continent.

The sipunculids were given the rank of a phylum first by Sedgwick (1898) and more recently by Baltzer (1931), Pickford (1947), and Fisher (1952).

II. Australian Species

1. Genus SIPUNCULUS Linnaeus

Diagnosis of genus (*based on Fisher* 1952).—Usually large animals with long cylindrical body and short, sharply differentiated introvert covered with squamiform, triangular papillae. Trunk generally thick-walled and longitudinal and circular muscle layers divided into regular bundles. Skin divided into rectangular areas by longitudinal and circular furrows. Posterior end of body rounded or bluntly pointed and sometimes marked off from the main trunk by a limiting ring fold of skin. A flat tentacular fold surrounds the oral disk and from its margin tentacles of varying complexity develop. Neither hooks on introvert nor papillae on trunk. Type, *Sipunculus nudus* Linn., 1766.

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(*a*) SIPUNCULUS ANGASI Baird

Figs. 1-4; Plate 1

Sipunculus angasi Baird, 1868, p. 76.
Sipunculus nudus Fischer, 1914, p. 1.
Sipunculus sp. Fisher, 1952, p. 376.

Specimens examined, 40.—QUEENSLAND (3 specimens): Dunwich, Feb. 1953, Prof. W. Stephenson; Line I., D. Mackellar (Aust. Mus., Sydney, G 11388); Hayman I., E. M. Embury (Aust. Mus., Sydney, G 3131). VICTORIA (8 specimens): Portarlington, 3.iii.1885 (Nat. Mus. Vic.); Brighton, 24.iii.1880, J. F. Bailey (Nat. Mus. Vic.); Black Rock, 30.x.1916, "on beach" (Nat. Mus. Vic.); Hobson's Bay, 24.viii.1891, "from channel", F. Clarke (Nat. Mus. Vic.); Victorian coast, 6.v.1910, A. Coles (Nat. Mus. Vic.); Rosebud, 21.ix.1932, D. Creswell (Nat. Mus. Vic.); Queenscliff, 1.v.1884, W. Jones (Nat. Mus. Vic.); Corio Bay, Jan. 1894, "found on beach", F.N.C. (Zool. Dept., Univ. of Melb.). TASMANIA (2 specimens): Seven Mile Beach, south Tasmania, Dec. 1951, E. R. Guiler. SOUTH AUSTRALIA (27 specimens): Henley Beach, St. Vincent Gulf, Aug. 1938, "washed up on beach", Prof. T. H. Johnston; Largs Bay, St. Vincent Gulf, 22.ix.1939, H. Andrewartha; Glenelg, St. Vincent Gulf, "lying on sandy beach, after storm", 4 specimens (Zoology Dept., Univ. of Adelaide); South Australian coast, 21 specimens (South Aust. Museum, Adelaide).

Previous Australian record.—SOUTH AUSTRALIA: Port Lincoln (Baird 1868).

Habitat

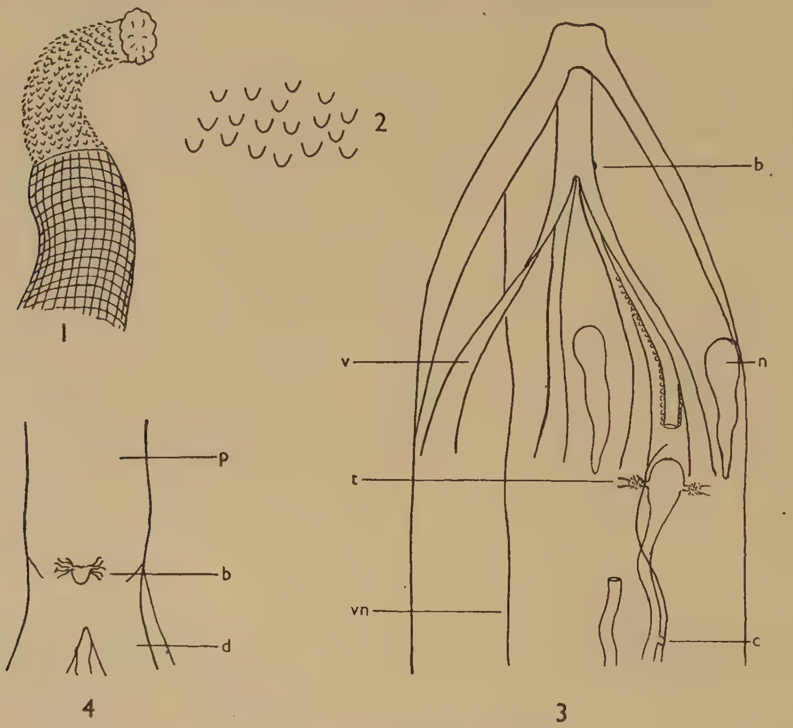
Most of the South Australian specimens were washed up on sandy beaches after storms. The species in South Australia apparently lives in sand below low tide level. In spite of numerous attempts the author has not yet been able to find a live specimen. Professor Stephenson of the University of Queensland, however, has been more successful. The specimen from Dunwich quoted in the above list was obtained by him while digging in "muddy sand just below the level of the low water spring tides".

Description

The specimens are long and cylindrical, brown, pink, or grey in the preserved state with a slight iridescence in some cases. Their length is 17-28 cm and width 1-2 cm. Externally the body is divided by the longitudinal and circular musculature into numerous small, rectangular areas. The introvert is 2-3 cm long and bears numerous, small, flat, triangular lappets similar to those described for *S. nudus*. The mouth is surrounded by a wrinkled or bushy tentacular fold. The posterior extremity of most specimens is either slightly rounded and swollen or sharply pointed.

There are 27-30, usually 28, well-developed longitudinal muscles which rarely anastomose except in the posterior 1-2 cm of the worm. Four stout retractors arise at the same level, the ventral pair from muscles 3-5 (2-5, 3-6, 2-6, 1-6) and the dorsal 9-11 (9-12, 9-13, 8-13).

The anterior region of the oesophagus is fastened to the dorsal retractors by thin mesenteries and the anterior part of the intestine is fastened by fine threads to the body wall to form the characteristic 'sipunculus loop'. The intestine and rectum are also attached to the body wall by filaments. The rectum is about 2-3 cm long and the anal aperture is situated just anterior to the point of fixation of the retractors. A strand of tissue arises from longitudinal muscle 9 on each side of the nerve cord and stretching across the base of the dorsal retractor is attached to the rectum at a point about 1 cm from the anus. A small tufted knob of tissue, the so called "buschelformigen Körper", lies on each of these strands near the rectum. In two specimens these tufted organs are reduced in size; in all other specimens, however, they are well developed. A small, globular diverticulum is present on the rectum. A spindle muscle which arises anteriorly near the anus is fastened posteriorly to the



Figs. 1-4.—*Sipunculus angasi.*
Fig. 1.—Anterior region.
Fig. 2.—Triangular lappets from proboscis.
Fig. 3.—Anterior region dissected.
b, brain; *c*, caecum; *n*, nephridium;
t, tufted organs ("buschelformigen Körper").
Fig. 4.—Brain. *b*, Brain; *d*, dorsal retractor; *p*, proboscis.

intestine; it makes contact with the intestinal diverticulum. Two contractile vessels (1 ventral and 1 dorsal) run along the oesophagus and bear numerous small villi. In some specimens the posterior extremities of the vessels are swollen into small elliptical or egg-like structures which contain coagulated fluid, probably blood.

The nephridia are long, extending posteriorly to the base of the retractors, and free. They open to the exterior between muscles 4 and 5 or 5 and 6.

The nerve cord in the posterior body region lies close to the body wall; in the anterior region this is not so. Two paraneural muscles arise at about the level of the nephridial openings and run alongside the nerve cord to the introvert. The brain is bilobed. From its surface arise somewhat laterally 2 thin sheets of tissue from which are given off a number of filaments or processes. These threads are clear and brittle and may be as long as 2 mm. Rather similar processes have been observed arising from the frons of *Sipunculus polymyotus* Fisher, 1947.

Systematic position

Fischer (1914, p. 1) identified a sipunculid from St. Vincent Gulf, S.A., as *Sipunculus nudus* Linn. In his report he says, "Die Exemplare vom Fuschou und vom St. Vincent Gulf besitzen beide am Rectum die büschelformigen Organe, auch erstreckt sich die Basis der Retractoren nur über drei bis vier Längsmuskelbündel" and remarks that in *S. nudus* the retractors usually span 6 or 7 muscles. The present material has been compared with specimens of *S. nudus* in the British Museum of Natural History and with specimens from U.S.A. The sipunculids from St. Vincent Gulf and the other localities listed above differ from *S. nudus* in the following respects: (1) the number of longitudinal muscles, (2) the span of the retractors, (3) the structure of the brain or frons, and (4) the presence of small caeca on the contractile vessels.

The specimens which form the basis of this study closely resemble *Sipunculus robustus* Keferstein, 1865, reported to be distributed in the Indo-Pacific region. Although Keferstein (1865*a*, 1865*b*) and Selenka (1883) stated that no tufted bodies are present in *S. robustus* both Augener (1903, pp. 314, 345) and Prashad (1936, p. 235) claimed that these structures appear in their specimens from (1) Amboina, Uvea, and Sydney (Cape York?) and (2) Mergui, the Nicobars, and the Andamans respectively. The present Australian material has been compared with two of Dr. Prashad's specimens from the Indian Museum. Although the specimens from the two countries are alike in some respects the Indian specimens do not possess the elaborate frons found in all the Australian material. In addition, the brain of the specimens of *S. robustus* collected by the John Murray Expedition is a simple structure (Dr. A. C. Stephen, personal communication). Consequently these Australian specimens must be considered as being different from *S. robustus*. Monro (1931) identified *S. robustus* amongst the sipunculids collected from Low I., Qld., by the

Great Barrier Reef Expedition. Unfortunately no anatomical details of the specimens are given in his records.

Baird (1868) identified two sipunculids from Port Lincoln, Spencer Gulf, S.A. as *Sipunculus angasi*. Baird's description makes no mention of the internal anatomy of the worms and no reference to *S. angasi* has appeared in zoological literature since 1868. Baird's two specimens, still in a reasonable state of preservation, have been made available for re-examination by the authorities of the British Museum. Both the specimens are juveniles. The body of one dissected specimen is 8.5 cm long and the introvert about 1 cm. Twenty-nine longitudinal muscles are present, the ventral retractors arise from muscles 3-5 and the dorsal from 9-12, and strands of fastening tissue connect the rectum and longitudinal muscle 9. Tufted bodies are just discernible and the nephridia open between muscles 5 and 6. The brain either is not well developed or has deteriorated during preservation. A few very small thread-like processes, however, arise from it. With this information as a basis the Australian specimens described above are being identified as *Sipunculus angasi* Baird. It is unfortunate that the type specimens lodged in the British Museum are juveniles. Two adult specimens, sent to the British Museum by the author, will help to give an additional picture of the species.

The specimen from Port Willunga, S.A., referred to by Fisher (1952, p. 376) as being "superficially like *S. nudus*" and belonging "to another, probably new, species" is *S. angasi*.

S. angasi is a large sipunculid allied to *S. nudus* and *S. robustus*. It possesses 27-30 longitudinal muscles, a pair of "tufted" organs or racemose glands near the rectum, two contractile vessels with small villi, and a brain from which arise a number of delicate and rather brittle processes, observable when a longitudinal incision is made anteriorly along the dorsal (anal) side of the animal.

Type.—In British Museum of Natural History, London.

Type locality.—Port Lincoln, Spencer Gulf, S.A.

Distribution.—South, south-eastern, and eastern Australia.

(*b*) SIPUNCULUS ROBUSTUS Keferstein

Sipunculus robustus Keferstein, 1865*b*, p. 196.

Australian records.—QUEENSLAND: Low I. (Monro 1931). NEW SOUTH WALES: Sydney (Augener 1903).

(*c*) SIPUNCULUS sp.

QUEENSLAND: Linden Bank (Monro 1931).

2. Genus XENOSIPHON Fisher

Diagnosis

Differing from *Sipunculus* in the following respects: an extra pair of muscles functioning as retractors and protractors arising from the posterior border of the introvert and inserted in front of the brain; rectum long and anus in front of the nephridiopores; spindle muscle arises posterior to anus from wall of rectum; gonad in the form of a long loop attached to rectum and body wall.

Type, *X. branchiatum* (Fisher, 1947) p. 360; Fisher, 1952, p. 377; Fisher, 1954, p. 312.

(*a*) XENOSIPHON MUNDANUM (Selenka & Bülow)

Fig. 5

Sipunculus mundanus Selenka & Bülow, 1883, p. 108.

Sipunculus mundanus Fischer, 1922, p. 5.

Specimens examined, 12.—NEW SOUTH WALES (8 specimens) : Off Sow and Pig Shoal, Port Jackson, April 1929, "dredged", Capt. Comtesso, 2 specimens (Aust. Mus., Sydney, W2679) ; Lord Howe I., 2 specimens (Aust. Mus., Sydney, G3950) ; Gunnamatta Bay (Aust. Mus., Sydney, W1753) ; Bermagui, 1928, W. Driscoll, 2 specimens (Aust. Mus., Sydney, W2534) ; Botany Bay, 20.iv.1927, "washed up after storm", Miss I. Wright (Aust. Mus., Sydney). VICTORIA (1 specimen) : Portland, 24.viii.1951, N. Learmouth (Nat. Mus. Vic.). WESTERN AUSTRALIA (3 specimens) : Cottesloe, July 1926 (Univ. of West. Aust.).

Previous Australian records.—NEW SOUTH WALES: Sydney (Selenka and Bülow 1883) ; Port Jackson (Fischer 1922).

Description

This sipunculid is long, cylindrical, and when preserved in alcohol, yellow, brown, or pink in colour. The length of the body is 13-28 cm and the width 0.7-1.0 cm. The body wall is divided by well-developed longitudinal and circular muscles into numerous rectangular areas. There are 27-30 longitudinal muscles which seldom anastomose. The introvert is relatively short, about 1-2 cm long, and bears numerous scale-like, triangular lappets of about uniform size. The tentacular crown consists of a pad-like or tufted mass of small tentacles. A narrow band about 2-3 mm wide on the introvert just posterior to the tentacles is smooth and bears no lappets. A noticeable external character is that the annulations caused by the circular muscles are much less marked on the dorsal surface of the posterior third of the worm. In most specimens this region is smooth. No papilliform bodies, like those described for *X. branchiatum* Fisher, 1947 could be found on the body surface. In most specimens there is a terminal knob, rounded and smooth with a small pore posteriorly.

Four retractor muscles arise at about the same level; the ventral pair from muscles 2-4 (1-3, 1-4) and the dorsal from 7-10 (7-11, 8-11) sometimes slightly obliquely. Two short, ribbon-like protractor muscles arise from the dorsal surface of the introvert near the frons and are fastened to the anterior body wall.

The oesophagus is long, straight, and attached by thin mesenteries to the dorsal retractors and by numerous fine threads to the body wall. Two contractile vessels with numerous caeca are attached to the anterior surface of the oesophagus. There is a short post-oesophageal or "sipunculus" loop in all the specimens dissected. The spirals of the intestine are fastened to the body wall by numerous short thread-like mesenteries. The anal aperture is about 1-2 cm anterior to the nephridial aperture. In some specimens the lips of the anus bear a few very small papillae. The rectum is long and closely attached to the body wall and there is a small intestinal caecum. A fine spindle muscle arises from the ventral surface of the

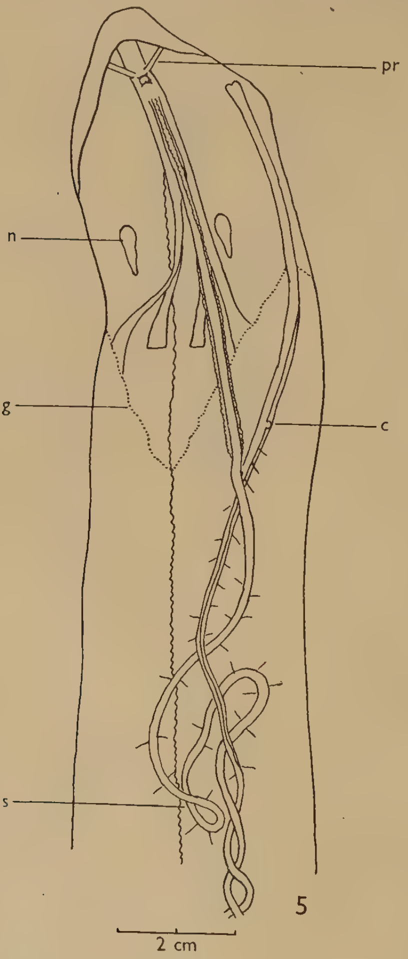


Fig. 5.—*Xenosiphon mundanum*. Anterior region dissected. *c*, caecum; *g*, gonadial strand; *n*, nephridium; *pr*, protractor muscle of the proboscis; *s*, "sipunculus" loop.

rectum and runs alongside the posterior region of the intestine. It makes contact with the caecum.

A fine, delicate thread of tissue arises on each side of the rectum near the point of fixation of the spindle muscle and runs along the body wall across to the dorsal retractor and onto the nerve cord at a point 2-4 cm below the point of attachment of the ventral retractors. It bears numerous minute, globular swellings. The nephridia in all the specimens examined are short (0.5-1.0 cm long), rather stout, and free. They open externally between muscles 4 and 5.

Two paraneural muscles arise at about the level of the nephridial openings. The brain is bilobed, about 1 mm long and 1 mm wide, and is capped anteriorly by a small mass of tufted tissue.

Transverse sections of the body wall show that the coelomic canals lie between the longitudinal muscles as in the genus *Sipunculus.*

Systematic position

This sipunculid corresponds very closely with *Sipunculus mundanus* Sel. and Bül., 1883, previously reported from New South Wales. Two of the specimens examined were collected from the type locality, Sow and Pig Shoal. Fisher (1947) erected a new genus, *Xenosiphon,* to accommodate a species, *Xenosiphon branchiatum,* which is closely related to *S. mundanus.* Subsequently Fisher (1954) emended his original diagnosis of the genus to include the Australian form formerly known as *Sipunculus mundanus.* Consequently these 12 specimens are regarded as *Xenosiphon mundanum.*

The anal aperture of *X. mundanum* is anterior to the nephridiopores. This fact distinguishes the species from related Australian species.

Type locality.—Sow and Pig Bank, Sydney, N.S.W.

Type specimen.—British Museum of Natural History.

Distribution.—Eastern, south-eastern, and western Australia.

3. Genus SIPHONOSOMA Spengel

Siphonosoma Spengel, 1912, p. 264.

Type, *Siphonosoma australe* (Keferstein); Gerould, 1913, p. 432; Fisher, 1950*b*, p. 805.

Diagnosis (*after Fisher* 1952)

Worms usually large with body resembling that of *Sipunculus.* Longitudinal muscles always separated into bands, the circular layer into anastomosing bundles (in most species). Larger species possess integumental coelomic sacs. Four retractor muscles. Intestinal spiral is fixed posteriorly by a spindle muscle which has 3 anterior roots. Dorsal contractile vessel with numerous villi or caeca. Nephridia with large crescentic nephrostomes. Paraneural muscles of the nerve cord less well developed than in *Sipunculus.* Numerous finger- or thread-like tentacles. Introvert without conspicuous scale-like papillae.

(*a*) SIPHONOSOMA CUMANENSE (Keferstein)

Figs. 6, 7

Phascolosoma cumanense Keferstein, 1867, p. 53.
Sipunculus cumanensis Selenka & Bülow, 1883, p. 104.
Siphonosoma cumanense Gerould, 1913.
Sipunculus deformis Baird, 1868 (from Sir C. Hardy I., north Australia).

Specimens examined, seven.—QUEENSLAND (5 specimens): Dunwich, Jan. 1950, Prof. W. Stephenson; Dunwich and Myora, 19.vii.1952, "common in mussel clumps", R. Domrov (2 specimens); Bird I. (2 specimens). NEW SOUTH WALES (1 specimen): Shelley Beach, mouth of River Clarence, Oct. 1938, A. Cameron (Aust. Mus., Sydney, W3194). WESTERN AUSTRALIA (1 specimen): North-west coast (collection from Univ. of West. Aust.).

Previous Australian records.—QUEENSLAND: Low I. (Monro 1931). WESTERN AUSTRALIA: Broome (Fischer 1921).

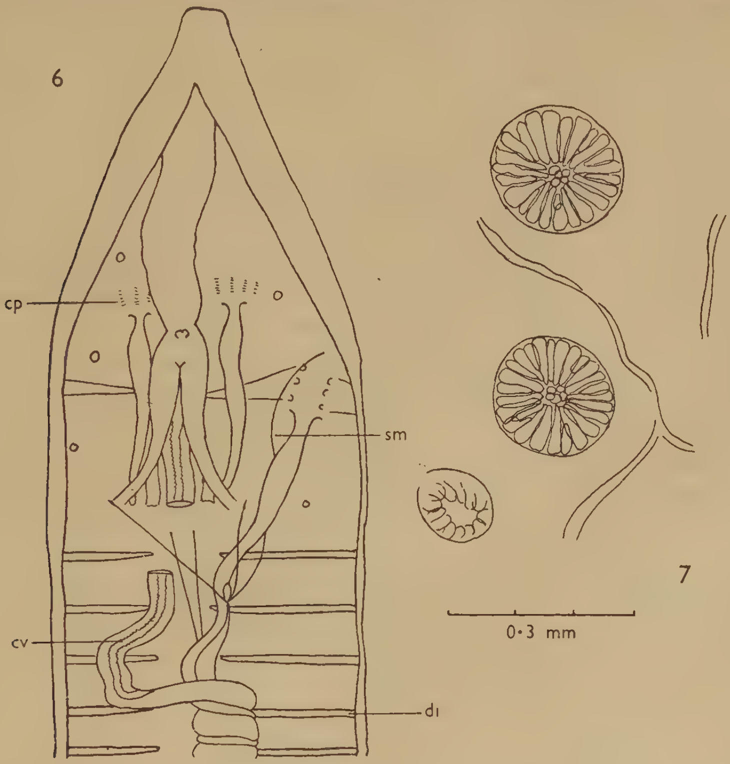
Description

The specimens are long, cylindrical, and slightly coiled. Their colour in alcohol is either brown or pinkish brown; one is slightly iridescent. The length of the body is 11-23 cm and the width, which is rather variable in some specimens, is 0.7-1.1 cm. The introvert of each of the specimens is retracted; in the smallest it is about 2 cm long and in the largest about 5 cm. No spines or hooks were found when the introvert was cut and opened out.

The whole surface bears skin bodies which vary considerably in size and appearance. The anterior surface of the introvert is divided by transverse and longitudinal furrows into numerous, small rectangular areas each enclosing a small, flat, circular, glandular opening about 0.1 mm in diameter. The skin bodies on the posterior part of the introvert are more papilliform, about 0.2 mm in diameter, and arranged approximately in transverse rows. On the anterior and posterior body surfaces the papillae are as much as 0.5 mm in diameter, circular to elliptical in shape, taller, and irregularly arranged. The largest papillae are composed of rather long, narrow plates lying with their long axis along the radii of the papilla. The tips of the papillae are dark brown and bear a small opening or pore. The skin bodies on the remainder of the body are much smaller; they are flat dark structures each possessing a minute pore. They lie in more or less longitudinal rows on the skin. The body wall is thick and opaque.

Eighteen to 20, usually 20, longitudinal muscles are present; they anastomose only slightly. Four retractors arise at about the same level; the ventral pair from muscles 2-3 (2-4, 1-4, 1-3) and the stouter dorsal pair from muscles 6-8 (6-7, 7-8). Numerous crescentic-shaped dissepiments occur transversely on each side of the nerve cord between the base of the retractors and the posterior extremity of the body. The points of attachment of the dissepiments vary in different specimens; they stretch between longitudinal muscles 1-8, 3-7, or 3-9.

The anterior region of the oesophagus is attached to the ventral retractors by thin mesenteries. A stout spindle muscle arises from the body wall anterior to the anus. It is attached to the posterior body wall by a number of longitudinally arranged mesenteries. Two roots are given off from the spindle muscle at a point just posterior to the intestinal caecum. They are attached to either muscles 8 or 9 at points just anterior to the left and right dorsal retractors. Two other fasteners arising from the same point on the last intestinal whorl are fixed symmetrically to longitudinal muscles 1 at the level of the ventral retractors. Anteriorly 2 strands of fastening tissue arising from muscle 1 at about the level of the anus stretch across the body wall and are attached to the wing muscle. They could be regarded as a part of an extended wing muscle. A single contractile vessel extends along the oesophagus to the first whorl of the intestine. It bears numerous villi or caeca.



Figs. 6, 7.—*Siphonosoma cumanense.*
Fig. 6.—Anterior region dissected. *cp*, Coelomic papillae; *cv*, contractile vessel; *di*, dissepiments; *sm*, spindle muscle.
Fig. 7.—Papillae from middle of body.

The gonads, as shown in one specimen, lie at the base of the ventral retractors. The nephridia are long, brown-yellow in colour, and attached to the body wall for about one-fifth of their length. The nephrostome lies between muscles 2-3 or 3-4 just in front of the anus. Internally a crescentic-shaped strand of tissue stretches at the nephrostome across 3 or 4 muscle bands. The nephridia extend as far as or just beyond the point of attachment of the retractors. A number of small, wing-like structures, the "coelomic papillae" (Fisher 1952), arise from the walls of muscles 1-6 just anterior to the nephrostomes. Oval bodies, 1.0-1.5 mm in diameter, are attached to the inner wall, especially in the anterior region of the worm. A prominent bilobed brain, about 2 mm long and 2 mm wide and without processes, is situated on the introvert near the point of attachment of the retractors.

Systematic position

These specimens, possessing body dissepiments and retractors which arise at the same level but lacking introvert spines and numerous rectal diverticula, fall into the subgenus *Damosiphon* Fisher, 1950*b*. They are considered to be *S. cumanense* (Keferstein), a species previously reported from Queensland and Western Australia. Keferstein (1867) stated that the length of the introvert is one-third that of the body. The ratio of the two lengths in these specimens is about 1 to 4 or 1 to 5.

Baird (1868) classified two sipunculids from northern Australia as *S. deformis*. The specimens are now lodged in the British Museum. One specimen, previously dissected, is about 13 cm long and possesses an introvert which in the retracted condition is 2-3 cm long. The body of the worm is constricted in a number of places. It possesses 20 longitudinal muscles and crescentic-shaped body dissepiments. The ventral retractors arise from muscles 1-4 and the dorsal pair at the same level from muscles 7-8. Small papillae are present on the anterior and posterior body surfaces. These specimens are considered to be *S. cumanense*.

S. cumanense possesses transverse body dissepiments readily discernible when the body wall is cut longitudinally. It differs from all other Australian members of the genus in this respect.

Distribution.—Western, northern, and eastern Australia. The species is recorded from many localities in the Indo-Pacific region, including East Africa, Mauritius, Zanzibar, Maldive and Laccadive Is., Malaya, Java, and Japan. Also West Africa and Florida.

(*b*) SIPHONOSOMA VASTUM (Selenka & Bülow)

Figs. 8, 9

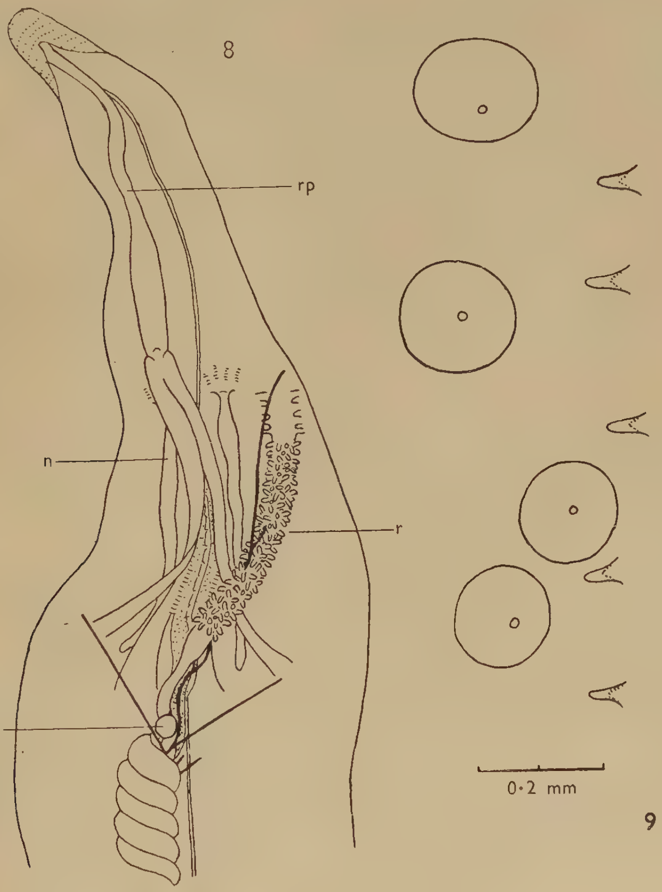
Sipunculus vastus Selenka & Bülow, 1883, p. 103.

Specimens examined, one.—QUEENSLAND: Outer Barrier Reef, Dr. W. J. Paradice (Aust. Mus., Sydney, W 1606).

Previous Australian records.—WESTERN AUSTRALIA: Shark Bay (Fischer 1919) and (Fischer 1926).

Description

Included in the Australian Museum collection is a large, cylindrical, straw-coloured sipunculid with a body about 26 cm long and an introvert, almost completely retracted, about 5-6 cm long. The introvert bears numerous transverse rows of spinelets about 0.1 mm long with yellow-brown, rather blunt extremities. The skin between the rows of spines is divided by fine furrows into small rectangular or polygonal areas which contain very small glandular openings. Rounded or hemispherical papillae are present on the posterior part of the introvert and in the anterior and posterior body surfaces. Those on the posterior region of the introvert are pale, small (0.1-0.3 mm in diameter) and arranged in more or less



Figs. 8, 9.—*Siphonosoma vastum.*
Fig. 8.—Anterior region dissected. *c*, Caecum; *n*, nephridium; *r*, rectum; *rp*, retracted proboscis.
Fig. 9.—Spines and papillae of proboscis.

transverse rows between the rows of spinelets. The papillae on the anterior body surface are larger (up to 0.6 mm in diameter) and brown in colour. Those near the introvert are arranged approximately in transverse rows but those nearer the anus are set more irregularly. On the posterior surface the papillae are about 0.5 mm in diameter.

Anteriorly there are 23 and posteriorly 26 longitudinal muscles. Two broad, stout ventral retractors arise from muscles 2-6 and 2 thinner dorsal retractors more anteriorly from muscles 9 on one side of the nerve cord and 10 on the other. The oesophagus is attached by thin mesenteries to the 2 ventral retractors. A contractile vessel with very small tubules lies along its dorsal surface. The thin-walled intestine of the specimen was filled with rather large, calcareous fragments. The most striking structure observed on dissection is the rectum. It is about 4.5 cm long and, except on the last 1 cm of its length, bears numerous, yellow, branching, finger-like villi or diverticula about 1-2½ mm long. The region of the rectum which does not bear diverticula (the part nearest the anus) is held firm by very well-developed wing muscles. The anal aperture lies between muscles 11 and 12 at about the level of the nephrostomes. A globular, sac-like diverticulum about 3-4 mm in diameter arises from the last whorl of the intestine.

A stout spindle muscle arises anteriorly from 3 main roots. One arises from muscle 12 at a point about 5 mm anterior to the anus and after joining a very short fastener attached to the rectum runs closely associated with the rectum to the intestinal diverticulum. Here it is joined by 2 other stout roots, one arising from muscle 11 just anterior to the left dorsal retractor and the other from muscle 8 just below the level of the right dorsal retractor. The spindle muscle is fastened posteriorly to a sheet of muscle arising from the body wall. The alimentary canal is held in position also by 2 other strands of fastening tissue. One, arising from the ventral surface of the intestine near the 2nd to last whorl, bifurcates near the body wall into 2 parts which are fixed to muscle 1 on either side of the nerve cord at about the level of the dorsal retractors. The other fastener, a thinner strand, arises from the last whorl. Unfortunately it was damaged during dissection and the point where it joins the body wall could not be determined.

The nephridia are thin-walled and brownish in colour. They arise between muscles 3 and 4 at the level of the anus and extend posteriorly as far as the point of attachment of the ventral retractors. The nephrostome is semi-lunar in shape and extends over 2 or 3 muscles. "Coelomic papillae" (Fisher 1952) are attached to muscles 2-6 in the vicinity of the nephrostomes. The nerve cord is a simple, thread-like structure pressed closely to the body along its entire length. No body dissepiments are present. The brain is a small bilobed structure without processes.

Systematic position

This specimen possessing numerous rectal diverticula and lacking body dissepiments belongs to the subgenus *Hesperosiphon* Fisher (1950*b*). It resembles very closely *S. vastum* (Sel. & Bül.) but differs from the latter as described by Selenka and Bülow (1883) and Augener (1903) in possessing small spinelets on the introvert.

Two species armed with hooks have already been assigned to the subgenus *Hesperosiphon;* they are *S. crassum* Spengel in Fischer (1919) and *S. parvum* Fischer (1922). This sipunculid from the Barrier Reef differs from *S. parvum* in the number and size of the rectal diverticula and in the arrangement of its spindle muscle and fasteners. The name, *S. crassum,* was given by Spengel, according to Fischer (1919), to a sipunculid from Western Australia. This information passed on to Fischer was never published by Spengel. All that is known about *S. crassum* is contained in Fischer (1919). As described "with reservations" by Fischer, *S. crassum* is closely allied to *S. vastum* but possesses introvert spinelets. The size of the spinelets and papillae of *S. crassum* is almost the same as those of this Queensland specimen. Fischer, however, gives few details about its internal anatomy. Apparently he had doubts about the validity of *S. crassum* as a species because when his report of 1919 was reprinted in Die Fauna Südwest-Australiens (1926) what he called *S. crassum* in 1919 became *S. vastum* in 1926. This means that Fischer considered that *S. vastum* might possess introvert spines. Another worker, Wesenberg-Lund (1937), has described some specimens with hooklets from the East Indies as *S. vastum.* This specimen from the Great Barrier Reef is therefore being recorded as *S. vastum.*

S. vastum is distinguished from *S. cumanense* and *S. australe* by the numerous caeca or diverticula found on its rectum. These structures are revealed when the animal is opened by a longitudinal incision through a point about 0.75 cm on one side of the anus.

Type locality.—Jaluit.

Distribution.—Mauritius, Great Barrier Reef, and north-west Australia. Marshall, Loyalty, Laccadive, and Maldive Is., New Caledonia, New Britain, and East Indies.

(*c*) SIPHONOSOMA AUSTRALE (Keferstein)

Phascolosoma australe Keferstein, 1865*b*, p. 197.
Sipunculus australis Selenka & Bülow, 1883, p. 90.
Siphonosoma australe Fisher, 1950*b*, p. 807.

Australian records.—NEW SOUTH WALES: Sydney (Keferstein 1865*b*); Sydney (Augener 1903).

Remarks

S. australe, as described by the above authors, unlike *S. cumanense,* possesses introvert spines and lacks numerous rectal diverticula as are found in *S. vastum.*

III. ACKNOWLEDGMENTS

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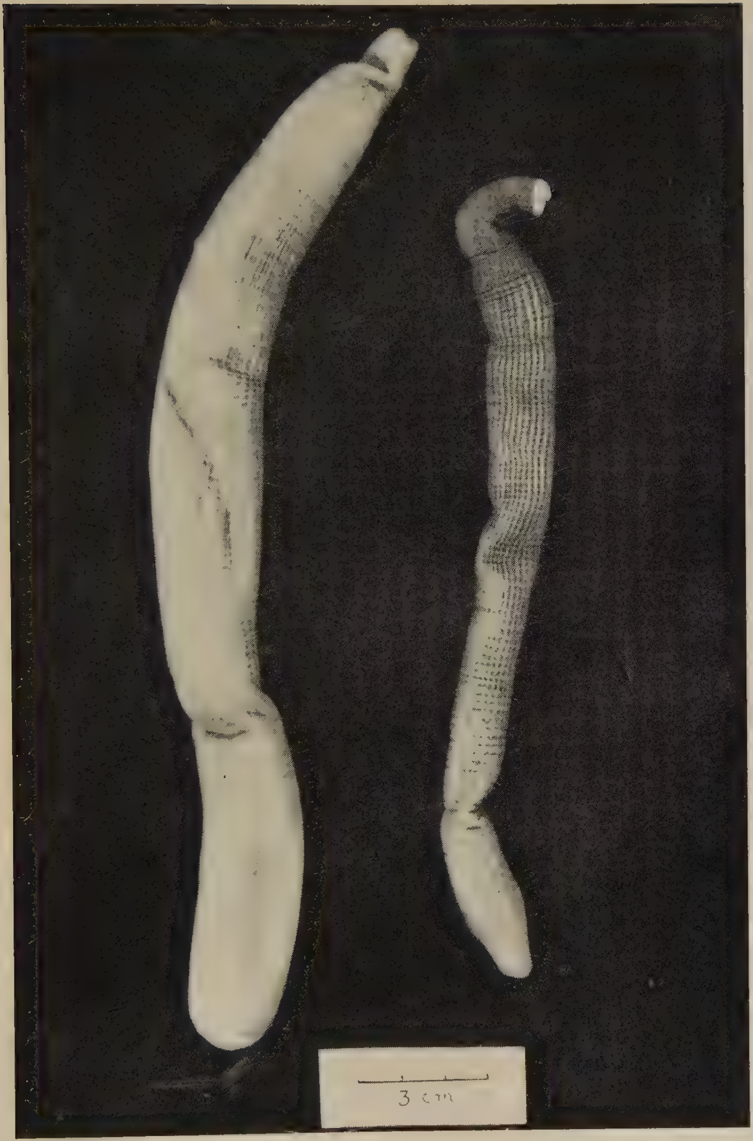
AUSTRALIAN SIPUNCULOIDEA. I



Sipunculus angasi. The larger specimen from St. Vincent Gulf, S.A.; the smaller from southern Tasmania.

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A REVISION OF THE AUSTRALIAN PEARL-SHELLS, GENUS *PINCTADA* (LAMELLIBRANCHIA)

By J. S. Hynd*

(*Manuscript received September 2, 1954*)

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Summary

Characters used in the taxonomy of pearl-shells are reviewed and their variation with age and environment is discussed. Extensive variations with age are revealed. The growth processes have proved to be the most distinctive and invariable criterion of species but are highly susceptible to erosion and mechanical damage. Other characters of major importance are the hinge teeth, general outline of shell, convexity, external markings, and internal shell margin. The soft parts are of little value in delineating species.

Phylogenetic relationships within the genus are considered. It is held that the lingah type of pearl oyster is the most primitive.

A key to the Australian species is given.

On the basis of the review of taxonomic characters, 31 trivial names occurring in a check-list of Australian species are rearranged under six specific headings. These synonymies are discussed, the species redescribed, and the geographical ranges reviewed.

I. Introduction

This critical revision of the systematics of the genus *Pinctada* has been pursued as a preliminary to the biological investigation of pearl-shell by the Division of Fisheries, C.S.I.R.O. A check-list of species recorded from Australian waters was found to contain 31 trivial names. Many of these were of doubtful standing and it was decided that a revision was desirable.

Collections were made from various localities on the tropical and subtropical Australian coast, particular attention being paid to localities from which species had already been recorded. This was supplemented by the examination of material in the Australian Museum collection, in particular the Barrier Reef Expedition specimens reported on by Iredale (1939).

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In addition the author has handled many thousands of living specimens growing under both natural and artificial conditions. The knowledge thus gained of the variation of the animals with age and in different environments has been of fundamental importance in separating the various species.

II. Taxonomic Characters

(*a*) *Shell Characters*

The shell characters on which the taxonomy of the pearl-shells is based are subject to wide variation. This variation can be attributed to a number of causes, of which geographical separation and ecological differentiation are important. In addition all species show marked changes in appearance with age. These variations have a tendency to follow well-defined lines and it is the purpose of the ensuing discussion to evaluate the degree and kind of variation that may be expected under different conditions.

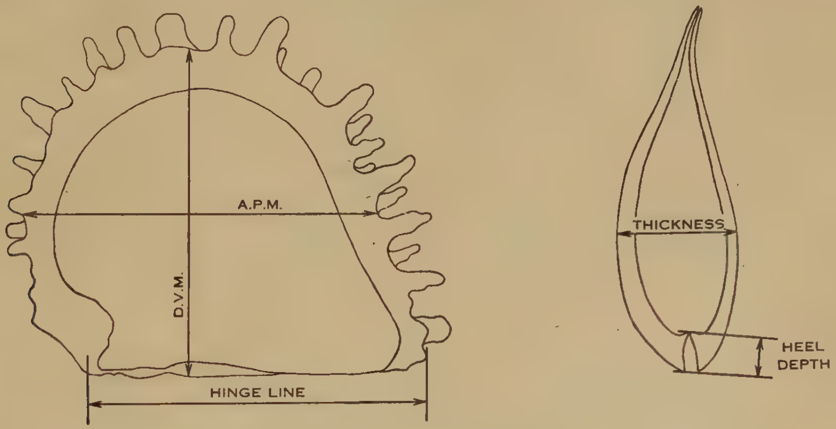


Fig. 1.—Diagrammatic drawing showing measurements referred to in the text. A.P.M., anteroposterior measurement; D.V.M., dorsoventral measurement. (Diagram drawn by I. S. R. Munro.)

Plate 1 has been prepared to assist in the identification of shell structures and regions, the names of which appear in the text. Figure 1 shows the various shell measurements also appearing in the text.

(i) *Form of Shell.*—Throughout the literature the terms "oblique" and "erect" have been used to describe the general form of the shell. These terms are rather vague, so to facilitate the accurate description of specimens and to permit of quantitative measurements, the concept of the "reference axis" is introduced. This axis (Plate 1, *ref. ax.*) is an imaginary line drawn from the umbo through the anterior edge of the adductor muscle scar to the distal border, following the curve of the rayed pattern on the external surface. It represents the locus of points secreted at successive intervals by the same portion of the mantle of the animal, and is invariably a *curved* line turning forward throughout its length. The angle between the tangent to the curve at its distal end and the hinge line, may be used as a criterion of the form of the shell.

When the angle is conspicuously less than a right angle the shell is "oblique", and when approximately a right angle the shell is "erect". When the tangent to the axis makes a conspicuously obtuse angle with the hinge line, as it does in some specimens, it is convenient to speak of these shells as "obtuse".

From the definition of the reference axis and the fact that this axis turns forward throughout its length, it follows that for any given specimen, the angle between the tangent and the hinge line *increases* with age. In other words the obliquity of the shell *decreases* with age. This is true for all normal specimens of all species.

Lison (1949) has shown that for a bivalve shell, of all the possible axes drawn in the manner of the reference axis only one lies completely in one plane. This he has called the "côte directrice" or directive axis. In pearl oysters this lies posterior to the reference axis and the reference axis is therefore a "côte non-directrice". Because of its unusual position in the pearl-shells, the directive axis has proved useless for descriptive purposes.

(ii) *Anterior Border.*—The shape of the anterior border and its position relative to reference points on the shell forms a valuable taxonomic character. Jameson (1901) found it convenient to draw a line at right angles to the hinge line through its anterior end, and indicated the proportion of nacre anterior to it. As the anterior ear is rather variable in size and is subject to damage, and as the anterior end of the hinge line is an ill-defined point, Jameson's line is not adopted. Instead a line drawn at right angles to the hinge line, through the byssal notch, is used and is known herein as the "reference line" (Plate 1, *ref. line*).

The proportion of nacre (if any) anterior to this line increases in all species with age. In very young *P. fucata* (Gould) the entire nacreous area lies posterior to the line but as growth proceeds and the shells become more erect, a greater or lesser amount projects in front of it. This progressive change is revealed by a comparison of the specimens in Plates 1 and 4. In specimens of *P. margaritifera* (Linnaeus) and *P. maxima* (Jameson) of about 2 cm dorsoventral measurement (D.V.M.) (see Fig. 1 for explanation of term), the anterior border of the nacre lies along or slightly anterior to the line. The area so cut off increases markedly with age, particularly in *P. margaritifera*.

The anterior non-nacreous border lies in front of the anterior nacreous border, and only in very young specimens of the more oblique species does the non-nacreous border lie behind the reference line.

In addition to changes in the position of the anterior border associated with changes in the obliquity of the shell, there appear to be other changes brought about by purely local intrinsic forces, e.g. in *P. margaritifera* there appears to be a "growing area" on the anterior border immediately below the byssal notch. Local growth in this area helps to produce the strongly convex anterior border characteristic of this species. Plate 2, Figure 2, shows a specimen in which this growing area is well defined.

(iii) *Anterior Ear and Byssal Notch.*—The anterior ear (Plate 1, *ant. e.*) or rostrum is a small more or less triangular area of the shell bounded dorsally by the hinge line, ventrally by the byssal notch, and posteriorly by a more or less vertical ridge on the internal surface of the nacre. The nacreous areas of the ears of the two sides are subequal but the non-nacreous border of the left ear extends in young specimens well in advance of that of the right side. The nacreous area of the ears relative to the rest of the shell decreases slightly with age. The non-nacreous area of the left ear also decreases relatively with age, becoming subequal to that of the right side.

The prominence of the ridge defining the posterior boundary (Plate 1, *p.b.e.*) varies considerably with age, and from specimen to specimen, for all species but in general the ridge tends to disappear with age.

The byssal groove (Plate 1, *by. gr.*) is a short forwardly curved depression on the external surface of the right valve running from the umbo to the byssal notch (Plate 1, *by. n.*). It represents the locus of former byssal notches. In young specimens of all species the byssal notch is a narrow cleft. This condition remains in old specimens of some species but in other species the notch (and the groove) widens with age. In *P. maxima* it disappears completely after the byssus is shed.

In all species except one, the ears of each side are arranged more or less symmetrically about the median plane of the animal. However, in *P. albina sugillata* (Reeve) the ears of both sides are twisted to the right to a greater or lesser extent and correspondingly the hinge line turns to the right at its anterior end.

(iv) *Posterior Border, Sinus, and Ear.*—Immediately below the hinge line, the posterior border is frequently indented by a sinus (Plate 1, *post. si.*) of greater or lesser depth marking off an area of the shell of corresponding extent known as the posterior ear (Plate 1, *post. e.*). Where the sinus is deep the posterior ear is relatively large and conversely. In specimens in which the posterior sinus is absent but that portion of the posterior border proximal to the hinge makes an acute angle with the hinge line, the enclosed area is also referred to as the posterior ear.

The variation of these structures, both from specimen to specimen and in any specimen with age, is greater than those of any other character and the taxonomic value of the structures is correspondingly small. In extremely young specimens (up to 1 month old) the posterior sinus, if any, is shallow. A very shallow sinus is visible in most of the specimens in Plate 4, Figure 1, Plate 6, Figure 1, and Plate 9, Figure 3. Specimens of this age of *P. maxima* and *P. margaritifera* have not been examined but growth rings on older specimens indicate that it is true for these species as for the others. With further growth the posterior sinus tends to deepen, up to a stage where backward growth of the hinge line practically ceases and the sinus becomes shallower again. Plate 10, Figure 1, shows a young specimen of *P. a. sugillata,* somewhat older than those shown in Plate 9, Figure 3, in which the sinus is well developed while Plate 12, Figure 1, shows a much older specimen in which the ear has completely disappeared. The angle made by the posterior border with the hinge line varies correspondingly with growth but can be used to a limited extent for taxonomic purposes.

As with the anterior border there appears to be a region of local growth in the posterior border in at least one species. This is located on the posteroventral margin, and disproportionate growth in this region produces in aging specimens of *P. a. sugillata* from certain localities a characteristic backward-curving shell. Plate 11, Figure 3, shows a specimen of *P. a. sugillata* in which this phenomenon is well marked.

(v) *Convexity of the Valves.*—Except in deformed specimens the left valve is more convex than the right. The right valve may be almost flat and its distal edge may even be concave. This condition is typical of young oysters with a relatively large and flexible non-nacreous border but it is sometimes retained in older oysters. The amount of concavity may also be varied by the oyster by contraction of the adductor muscle which, by bringing the two valves tightly together, causes the flexible lip of the right valve to fit itself to the convexity of the left valve. This condition is commonest in *P. fucata.*

(vi) *Growth Processes.*—The growth processes (Plate 1, *gr. pr.*) are small scale-like projections from the external surface of the shell. They are laid down by the animal at successive intervals at the distal border, and with increase in size they are relegated to the external surface. They are arranged in a pattern consisting fundamentally of concentric circles and radial rows. They are subject to erosion and mechanical damage, and are frequently absent except around the lip of the shell.

They attain their strongest development and characteristic form only in specimens which have grown under optimum conditions. Under these conditions they clearly exhibit characters diagnostic of the species.

The number of processes or rows of processes is not constant within a species, varying both from specimen to specimen and in each specimen with age. Except in abnormal specimens the number increases with age.

In several species the growth processes bear transverse markings of various types which are useful as diagnostic characters. These markings are clearly visible in the specimen illustrated in Plate 1, and possibly represent increments in the formation of the processes.

(vii) *Hinge Teeth.*—The hinge teeth (Plate 1, *a.h.t.* and *p.h.t.*) consist of paired elevations of the nacre of the hinge line anterior and posterior to the ligament. The anterior (cardinal) pair appear as small, rounded or oval bodies situated in advance of the umbonal recess. They are invariably asymmetrical, that of the right side having the strongest development. The posterior (lateral) pair appear as elongated ridge-like bodies running from near the posterior end of the ligament backwards and slightly downwards onto the surface of the nacre. They are sometimes asymmetrical.

In some species which possess hinge teeth in the young, the teeth tend to become obscured with age. In others the teeth are more strongly developed in the adult. Some species never possess hinge teeth even in the young.

(viii) *External Colour and Markings.*—The external markings of the shell consist typically of a series of prominent, radially arranged rays running from the umbo to the distal border and diverging throughout their length. These rays are apparent as alternate bands of different colours, or alternate light and dark shades of the same colour. As a modification of this arrangement the rays may be broken up into a series of discontinuous patches, or further reduced to irregularly distributed flecks of colour. In some specimens rays may be completely absent and in this case the external surface usually exhibits slight gradations in tint of one colour.

These various colour patterns may occur not only in the one species but in the one specimen. Plate 5, Figure 1, shows a series of *P. fucata* in which several different colour patterns have been assumed at different stages of growth.

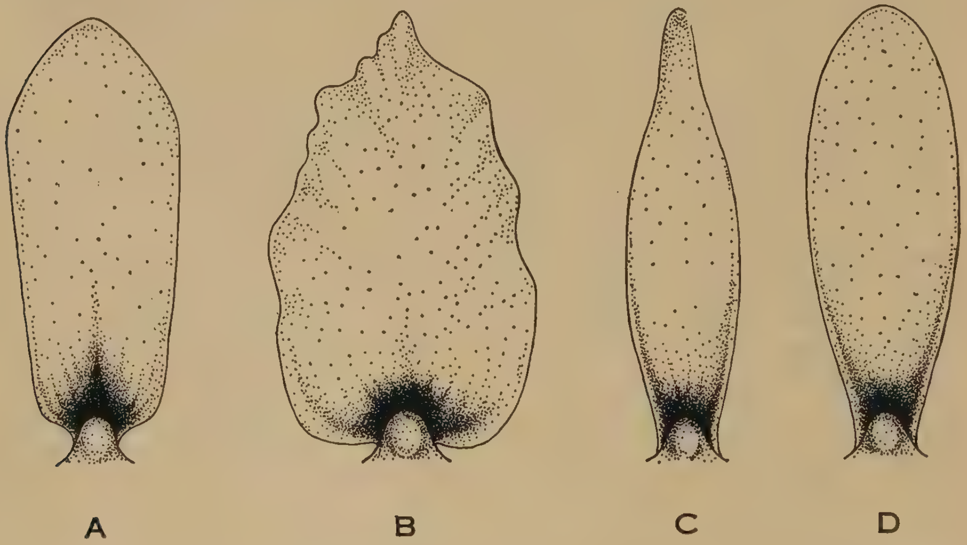
In some species a relationship may be traced between the colour pattern of a shell and the superimposed growth processes. In *P. maxima* and *P. margaritifera* the coloured rays are formed by the basal portions of broken-off growth processes, in *maxima* darker than the ground colour, in *margaritifera* lighter.

(ix) *Colour of Nacre and Internal Margin.*—True colour in the nacre, as distinct from iridescence, develops in nearly all species under certain conditions. In *P. maxima* and *P. margaritifera* this colour develops only at the distal border and gives the valves the characteristic appearance indicated by the colloquial names "golden- and black-lipped pearl-shell". In the other species colour in the nacre develops (if at all) over the whole of the nacre. It ranges from greenish yellow to dusky orange and its development is associated with aging of the individual.

The non-nacreous internal margin of the shell often shows patches or bands of colour which are of taxonomic value. The patterns are of two types — radial rays corresponding to the external radial rays, and circular bands or irregular patches independent of the external coloration. Sometimes both are present in the one individual and then the radial pattern is always the more distal. Circular patterns appear in *P. maculata* (Gould) and *P. a. sugillata.*

(*b*) *Soft Parts*

The systematics of the pearl oysters is, as with most other Mollusca, based exclusively on shell characters. However, Herdman (1904) in his description of the anatomy of *P. vulgaris* (= *fucata*) from Ceylon, draws attention to one character — the shape of the anal funnel — in which his material differed from other species.



DEL. I.S.R. MUNRO

Fig. 2.—Anal funnels of several Australian species of pearl-shells. *A*, *Pinctada maxima* (Jameson); *B*, *P. margaritifera* (Linnaeus); *C*, *P. fucata* (Gould); *D*, *P. albina sugillata* (Reeve).

The author has examined this and other characters in the several species available and is able to confirm its value as a specific character. Other characters investigated did not yield such definite results.

(i) *Anal Funnel.*—The anal funnel is a contractile flap-like process of uncertain function attached to the posterior lip of the anus. Contraction of the intrinsic muscles causes the organ to curl up and alteration of the outline results, but nevertheless it is possible to distinguish a more or less typical shape for each species.

The anal funnels of four Australian species are shown in Figure 2. That of *P. maxima* is regular in outline and wider distally than proximally. That of *P. margaritifera* is wider proximally than distally and very irregular in outline, sometimes lobate. However, Australian specimens never attain the remarkable palmate form shown by Herdman (1904, Plate 3, Fig. 5). That of *P. fucata* is relatively narrow and pointed while that of *P. a. sugillata* is wider and rather more oval. In all species there is considerable variation and irregularly lobate funnels frequently occur.

(ii) *Gill Filaments.*—Counts were made in a few specimens of four Australian species of the number of gill filaments in a plica (see Herdman 1905 for explanation). In each specimen the count varied from plica to plica and consequently the condition for an individual must be expressed as a range. The range for each species is tabulated below. In most cases the individual range approached that of the species.

TABLE 1

GILL FILAMENTS PER PLICA IN AUSTRALIAN SPECIES OF PINCTADA

Species	Gill Filaments per Plica
P. fucata	10-15
P. a. sugillata	8-13
P. maxima	8-15
P. margaritifera	13-18

This preliminary investigation shows that, with the possible exception of *P. margaritifera,* the character is of little value in separating the species. It is possible that more extensive investigation may reveal significant statistical differences.

(iii) *Velar and Mantle Processes.*—A preliminary inspection of four of the Australian species did not reveal any important differences.

(iv) *Union of Ventricle and Rectum.*—No divergence from the condition recorded by Herdman (1904) and White (1942) for *P. vulgaris* (= *fucata*) from Ceylon was observed in Australian species.

(v) *Interauricular Junction.*—The condition in Australian species is the same as that recorded by Herdman (1904) and White (1942) for *P. vulgaris* (= *fucata*).

III. GENERIC NAME

Prashad (1932) and Iredale (1939) have shown that *Pinctada* Röding has priority over other generic names.

IV. GENERIC SUBDIVISIONS AND PHYLOGENETIC RELATIONSHIPS

Jameson (1901) made a broad subdivision of the genus on the presence or absence of hinge teeth. In the section without hinge teeth he placed the species *Margaritifera maxima* and *M. margaritifera*. In the section with hinge teeth he placed the rest of the species, subdividing them again on the form of the shell.

These subdivisions are taxonomically and phylogenetically fundamental but the character chosen by Jameson as the basis for his primary subdivision is important only because it is correlated with major variations in shell form and other characters.

The complete absence of hinge teeth in Jameson's Division I is correlated with: a shell form which is erect in the young; the presence of growth processes which are relatively large, parallel-sided, and longer than broad; the development of colour in the nacre in a band around the distal edge; a relatively large adult shell size. The presence of hinge teeth in Division II is correlated with: a shell form extremely oblique in the young; the presence of growth processes which are relatively smaller and of various shapes; the uniform development (if any) of colour in the nacre; small to medium adult shell size.

As an oblique shell form and the presence of hinge teeth are characters shared by the majority of the Pteriidae, it must be considered that Jameson's Division II contains the more primitive species.

The more important characters on which Jameson's second subdivision is based are the obliquity and convexity of the shell and the degree of development of hinge teeth. Investigation shows that they can be correlated with important differences in the growth processes. Setting aside *P. capensis* (Sowerby), the relationships of which are obscure, the rest of the species fall into two groups. In the first group (Section *b* of Jameson) the shell is erect to obtuse in the adult and flat to moderately convex, the hinge teeth are usually lost with age, and the growth processes are parallel-sided and moderate in size and number. In the second group or lingah type of pearl oysters (Section *c* of Jameson) the shell is typically oblique and convex, the hinge teeth are frequently retained throughout life, and the growth processes are small, tapering, and numerous.

The lingah pearl oysters, in their convexity, obliquity, and retention of hinge teeth, approach closest to the condition found in the Pteriidae in general so that they must be regarded as the most primitive of the pearl oysters. Concerning the associated character of small, pointed growth processes, it is probable that this also represents an ancestral condition since in most pteriids, growth processes tend to be of that size and shape.

V. Key to Australian Species

The following key is offered as a tentative solution to the problem of rapid and accurate identification of specimens. Because of the extreme variability of the species it has proved impossible to draft a key that permits of the identification of all specimens. In particular, much difficulty will be experienced if the key is used to identify very young individuals.

The task has been made more difficult as the growth processes, which are the best identifying character in all species, are frequently damaged or absent, and have largely been excluded from the key. They have been used only where no other useful differential character could be found.

KEY TO AUSTRALIAN SPECIES OF THE GENUS PINCTADA

1. Hinge with teeth 2
Hinge without teeth 3

2(1). Posterior hinge tooth consisting of a single ridge. (Nacreous area of valves not markedly unequal. Posterior ear small or absent) 4
Posterior hinge tooth consisting of a double ridge. (Nacreous area of valves not markedly unequal. Posterior ear small or absent) 5
Posterior hinge tooth flat, facet-like. (Nacreous area of valves markedly unequal. Usually a very large posterior ear) .. .. *chemnitzi*

3(1). Anterior non-nacreous border projecting a considerable distance anterior to reference line 6
Anterior non-nacreous border projecting only slightly or not at all 7

4(2). Growth processes broad, rounded. (Hinge line often turns strongly to right at anterior end) 11
Growth processes small, pointed. (Hinge line usually straight at anterior end) 5

5(2 & 4). Non-nacreous margin with white, porcellanous patches. (Nacre usually with golden tint. Growth processes opaque white or horny) .. .. .. *maculata*
Non-nacreous margin without white, porcellanous patches. (Nacre without golden tint. Growth processes nearly always with transverse dark and light bands, sometimes horny) .. .. *fucata*

6(3). Edge of nacre conspicuously dark, usually with a distinct yellow tint proximally. (Shell moderately large and heavy in adult. Non-nacreous border usually dark) .. .. *margaritifera*
Edge of nacre golden in colour. (Shell large, heavy. Non-nacreous border horny) .. .. *maxima*
Edge of nacre without colour. (Shell small to large in adult. Border dark to horny) 8

7(3). Edge of nacre without colour. (Shell small to large) 9
Edge of nacre golden in colour. (Shell large, heavy) .. .. *maxima*
Edge of nacre conspicuously dark, usually with distinct yellow tint proximally. (Shell moderately large and heavy) .. .. *margaritifera*

8(6). Shell large, heavy. (Non-nacreous border horny) .. .. *maxima*
Shell small, light. (Non-nacreous border sometimes horny, often with a narrow black band immediately distal to nacre, occasionally dark) 11

9(7). Shell large and heavy .. .. *maxima*
Shell small and light 10

10(9). Growth processes broad, rounded, rarely with transverse bands. (Hinge line often turns strongly to right at anterior end) 11
Growth processes small, pointed, usually with transverse dark and light bands. (Hinge line usually straight at anterior end) .. .. *fucata*

11(4, 8, & 10). External surface of shell pale grey or yellow. (No black band immediately distal to nacre) .. .. *albina carchariarum*
External surface of shell rayed or dark. (Usually a black band immediately distal to the nacre) .. .. *albina sugillata*

VI. DESCRIPTION OF SPECIES

PINCTADA MARGARITIFERA (Linnaeus)

Plate 2, Figs. 1, 2

(*a*) *Synonymy*

Mytilus margaritiferus Linnaeus, 1758, p. 704.
Meleagrina radiatus Saville-Kent, 1890*a*, p. 3; 1890*b*, pp. 1, 8.
M. fucatus Saville-Kent, 1890*a*, p. 3.
M. Cummingii Saville-Kent, 1890*a*, p. 3.
M. cumingii Saville-Kent, 1890*c*, p. 543.
M. nigro-marginata Saville-Kent, 1893, p. 213, pl. 37.
M. Cumingii Saville-Kent, 1897, p. 212.
"Black-lip pearl shell" Pace, 1899, p. 11. Roughley, 1936, p. 220.
Pteria (*Margaritifera*) *margaritifera* var. *typica* Jameson, 1901, p. 374.
Meleagrina margaritifera Hedley, 1910, p. 344.
Pinctada margaritifera Hedley, 1916, p. 155; 1924, p. 6. Yonge, 1930, p. 164. Nicholls, 1931, p. 26. Hynd, 1950, p. 69.
P. nigromarginata Iredale, 1939, p. 335. Allan, 1946, p. 81; 1950, p. 226.

(*b*) *Discussion*

Prior to Jameson (1901), authors had been confused as to the correct application of *margaritifera* Linnaeus. Jameson re-examined Linnaeus's types and found that both specimens were "black-lipped" shells. Accordingly he applied *margaritifera* to that species and separated the "gold- or silver-lipped" species under the name *maxima*. Von Martens (1889, p. 190), Saville-Kent (1890*a*, p. 3; 1890*c*, p. 543; 1893, p. 207; 1897, p. 196), and Collett (1900, p. 2) had applied *margaritifera* Linnaeus to the "gold- or silver-lipped" shell. Regarding the "black-lipped" shell, Saville-Kent (1890*a*) stated that *radiatus, fucatus*, and *Cummingii* "represent names that have separately been applied to it by different authorities". In subsequent papers he used *radiatus* (1890*b*), *cumingii* (1890*c*), *nigromarginata* (1893), and *Cumingii* (1897) for the same species. Griffin (1886, p. 434) applied *margaritifera* to the Shark Bay shell (= *carchariarum* Jameson). Pace (1899) recognized that *margaritifera* Linnaeus should be applied to the "black-lipped" species but did not give a name to the "gold- or silver-lipped" species. In September 1901 Hedley listed *margaritifera* without diagnosis, and since it is unlikely that he would have seen Jameson's paper which appeared in April of that year, it is assumed that he referred to the "gold- or silver-lipped" shell.

Subsequent to Jameson (1901), authors have used *margaritifera* Linnaeus for the "black-lipped" species with the exception of Iredale (1939) and Allan (1946, 1950). Iredale revived *nigromarginata* Saville-Kent for Barrier Reef specimens of the "black-lipped" shell and in this he was followed by Allan. However, the present author is of the opinion that the characters given by Iredale for Barrier Reef specimens are not of specific rank and therefore *nigromarginata* Iredale must pass into the synonymy of *margaritifera* Linnaeus.

(*c*) *Description*

(i) *Form of Shell.*—Specimens of less than 2 cm D.V.M. have not been observed but above this size the shell is usually erect or obtuse, the obtuseness increasing with age. Growth lines around the umbo of certain specimens indicate that the very small specimens are moderately oblique though less so than other species.

In the adults anteroposterior measurement (A.P.M.) approximately equals D.V.M. in normal specimens but not in Barrier Reef specimens. In these, A.P.M. is usually less than D.V.M. (see Fig. 1 for explanation of terms).

(ii) *Anterior Border.*—The extension of the anterior border in advance of the byssal notch is most marked in adults. Jameson (1901, p. 373) gives 1/5 as the proportion of the total nacreous area in advance of this line. This proportion has been confirmed for normal adult specimens in the present study. Iredale (1939, p. 335) states that the anterior border scarcely projects in specimens from Australian coral reefs. This is true only for young or deformed specimens.

(iii) *Anterior Ear and Byssal Notch.*—In young specimens the non-nacreous portion of the left anterior ear extends a considerable distance in advance of that of the right side as in the specimen figured in Plate 2, Figure 1. The ears are not twisted and the byssal notch is directed anteriorly. With age the ears become subequal and the byssal notch increases transversely until in old specimens it gapes widely as in the specimen figured in Plate 2, Figure 2. This is correlated with the retention and strong development of the byssus throughout life.

(iv) *Posterior Border.*—In no specimens examined was there more than a slight sinus in the posterior border and therefore a posterior ear is absent. In the majority of specimens the posterior border is slightly convex and meets the hinge line at approximately a right angle. There is a slight tendency for this angle to increase with age.

(v) *Convexity.*—The left valve is moderately convex, the right valve is slightly less so, never flat. The convexity increases with age.

(vi) *Growth Processes.*—Typically these are long, parallel-sided structures with rounded or tapering ends as in the specimens figured in Plate 2. In section they are flat at their base, concave, twisted, or curled up at their tips. They may be arranged discretely or project from a continuous lamina. They are more or less straight throughout their length except for the tips, which curve slightly downwards and inwards. They are arranged in radial rows and lie relatively flat on the surface of the valve. Typically they are opaque white at the base, deepening to a bronze or black colour at the tips, and may show parallel transverse markings.

(vii) *Hinge Teeth.*—There is no trace of hinge teeth at any stage of development.

(viii) *External Colour and Markings.*—Externally the valves show a radial pattern of discrete or partially continuous white spots against a background colour of dark green, bronze, brown, or black. In very young specimens the ground colour is often quite light and the white rays not well marked, but with age the ground colour deepens and the rays become more prominent. The white spots represent the basal portions of old growth processes.

(ix) *Colour of Nacre and Internal Margin.*—Distally the nacre is a dark smoky colour with a hint of red and green iridescence. Immediately proximal to this dark border a distinct yellow infusion frequently appears. The body of the nacre is clear but never as lustrous as in *P. maxima.* The non-nacreous border is usually very dark with a few lighter markings.

(x) *Size.*—Specimens from Torres Strait are slightly larger than specimens from the more southerly localities of the Barrier Reef, which are usually deformed or stunted in their growth. The largest specimen seen by the author from Torres Strait measured 17 cm D.V.M. and 2.5 cm heel depth. Heavier specimens are known to occur.

(*d*) *Distribution*

Jameson (1901, p. 374) gives the Australian range for this species as "all along N. coast; E. coast as far south as Moreton Bay; W. coast to about 29°S." Jameson's specimens from Moreton Bay were from the Museum Cuming and presumably were accurately labelled. Iredale (personal communication) has seen a single specimen from the Amity Banks, Moreton Bay. The author has not seen any material from Moreton Bay.

The species occurs most prolifically on coral reefs just above or below low water springs. Occasional specimens are taken in deeper waters. The author has seen specimens from Torres Strait from water of 22 fm depth.

PINCTADA MAXIMA (Jameson)

Plate 3, Figs. 1-3

(*a*) *Synonymy*

Meleagrina margaritifera von Martens, 1889, p. 190. Saville-Kent, 1890*a*, p. 3; 1890*c*, p. 543; 1893, p. 207, pl. 38; 1897, p. 196. Hedley, 1901, p. 18.

"Silver- and golden-lip pearl shell" Pace, 1899, p. 11. Roughley, 1936, p. 220.

Meleagrina anomioides Melvill and Standen, 1899, p. 183. Hedley, 1910, p. 344. Iredale, 1939, p. 339.

Avicula (Meleagrina) margaritifera Collett, 1900, p. 2.

Pteria (Margaritifera) maxima Jameson, 1901, p. 377. Odhner, 1917, pp. 8, 15.

Meleagrina maxima Saville-Kent, 1905, p. 3. Hedley, 1910, p. 344.

Pinctada maxima Hedley, 1916, p. 155; 1924, p. 6. Yonge, 1930, p. 164. Iredale, 1939, p. 335. Allan, 1946, p. 81; 1950, p. 266, pl. 1, fig. 1. Hynd, 1950, p. 69.

(*b*) *Discussion*

As noted under *P. margaritifera* this species was first distinguished taxonomically from the "black-lipped" shell by Jameson (1901).

Melvill and Standen (1899, p. 183) have recorded from Torres Strait a single specimen of *M. anomioides* (Reeve). This record is listed by Hedley (1910, p. 344). Iredale (1939, p. 339) suggests that the specimen seen by Melvill and Standen was a young example of *P. maxima* and the present author agrees.

(*c*) *Description*

(i) *Form of Shell.*—The author has not observed specimens of less than 2 cm D.V.M. At this size the shell is already erect though growth lines on these young shells indicate that very young specimens are more oblique.

In half-grown specimens A.P.M. is approximately equal to D.V.M. but becomes increasingly less than D.V.M. with age.

(ii) *Anterior Border.*—Even in young shells the anterior border projects in front of the reference line but the area of nacre in advance of this line is not as extensive as in *P. margaritifera* and only increases slightly with age.

(iii) *Anterior Ear and Byssal Notch.*—The anterior ears are moderate in size and not twisted. The byssal notch in the right valve disappears in shells over about 15 cm D.V.M. coincident with the sloughing of the byssus.

(iv) *Posterior Ear.*—It is characteristic of this species that in young specimens the posterior border nearly always makes an acute angle with the hinge line, forming a prominent posterior ear. This feature is visible in the specimen figured in Plate 3, Figure 1. There may or may not be a sinus in the posterior border. As growth proceeds the hinge line shortens relative to the other measurements and the posterior ear disappears, with the result that in mature specimens the posterior margin meets the hinge at almost a right angle. In extremely old specimens growth of the hinge practically ceases while the posterior margin continues to develop, so that the posterior margin makes an obtuse angle with the hinge line.

(v) *Convexity.*—The left valve is moderately convex, the right valve flat to slightly convex. The convexity decreases slightly with age.

(vi) *Growth Processes.*—In young specimens the growth processes take the form of long, irregularly clavate, twisted structures up to $\frac{1}{3}$ the diameter of the shell in length. They are discrete, even sparse, in their distribution, and curve outwards from the surface of the shell at their proximal ends, downward and inward at their distal ends. In section they may be convex, concave, flat, or irregular. Typically they are arranged in radial rows though the irregularity of their shape and the sparseness of their distribution tend to obscure this fact. The specimen figured in Plate 3, Figure 1, shows the characteristic shape, size, and arrangement.

In mature specimens the processes are relatively smaller, and parallel-sided or tapering to a blunt point. In section they are flat at the base and concave throughout their distal half and curve downwards and sometimes inwards at their distal ends. They preserve the radial rows and discrete arrangement. The distal processes of opposite valves frequently interdigitate.

In ground colour the processes resemble the fawn coloured external surface of the shell with the exception that specimens with dark-coloured umbones have processes of the same colour in that region. In addition a pattern of red to reddish brown, parallel, evenly spaced, curved, transverse markings sometimes appears on the processes. These markings can be clearly seen in Plate 3, Figure 3.

(vii) *Hinge Teeth.*—Hinge teeth are completely absent in both young and old specimens. Jameson (1901, p. 379) on information supplied by Pace states that they are sometimes present in very young specimens but this has not been confirmed by the present author. The ridges noted by Jameson (loc. cit.) as possible remains of hinge teeth are almost certainly secondary structures appearing with age.

(viii) *External Colour and Markings.*—Usually the external surface of the shell is a uniform light fawn with no trace of radial markings. In some specimens, however, the umbonal region is coloured green, dark brown, or purple and is frequently marked with rows of spots of a deeper shade of the same colour. These spots represent the basal portions of broken-off growth processes. Plate 3, Figure 2, shows a dark green specimen in which the radial rows are clearly marked.

(ix) *Colour of Nacre and Internal Margin.*—The nacre is of a rich, clear lustre far surpassing any other species. It rarely shows any dark tints but at the distal border a rich golden band of varying width may develop. These "gold-lip" shells occur in varying proportion in shell from different areas. Shell taken in Torres Strait and New Guinea waters frequently contain over 50 per cent. gold lip. The width of the golden lip is also variable. In a specimen from Torres Strait seen by the author ¾ of the nacreous surface was of a rich golden hue, but such specimens are rare. Specimens from Western Australian and Northern Territory waters frequently contain a high percentage of gold lip but the golden edge is not as wide as in Torres Strait specimens and is often quite inconspicuous. Pace (1899) believes that a change from gold to silver lip and vice versa can, and does, occur.

The internal non-nacreous margin is clear and horny without colour or pattern.

(x) *Size.*—This is the largest of the Australian species. Jameson (1901) gives as the weight of old specimens 10 or more lb per pair. This is unusually high, the average weight of old specimens from Torres Strait being approx. 5 lb per pair.

Iredale (1939) records a specimen from Torres Strait measuring 250 by 282 mm. Specimens of this size are rare.

The heaviest specimen yet seen by the author measured 5.0 cm in heel depth.

(*d*) *Distribution*

Jameson (1901, p. 379) gives the Australian distribution as "all along N. coast of Australia; E. coast as far as Townsville (but not in quantities anywhere south of Cooktown); W. coast as far as 20° south in payable quantities and sparingly as far south as 25°". These two latitudes correspond to Port Hedland and Shark Bay respectively. The author is able to extend the eastern range for payable quantities of shell to Snapper I. — 16° 30′ S. — this locality having yielded a quantity of shell in recent years.

The species has been taken from low tide level down to about 40 fm. There is no record of specimens from deeper water than this. Specimens are occasionally found on reef flats just above low water springs but rarely in any quantity. The bulk of the commercial catch is taken in waters of 5-30 fm.

PINCTADA FUCATA (Gould)

Plate 1; Plate 4, Figs. 1, 2; Plate 5, Figs. 1-3

(*a*) *Synonymy*

?"Die perlenmuttermuschel" Chemnitz, 1785, p. 126, pl. 80, fig. 717.
?*Perlamater vulgaris* Schumacher, 1817, p. 108, pl. 20, fig. 3.
Avicula fucata Gould, 1850, p. 309; 1852, p. 441, figs. 551, 551*a*.
A. lurida Gould, 1850, p. 310; 1852, p. 440, figs. 550, 550*a*.
A. perviridis Reeve, 1857, pl. 8, sp. 20.
A. lacunata Reeve, 1857, pl. 10, sp. 29.
A. aerata Reeve, 1857, pl. 10, sp. 32.
Meleagrina aerata Paetel, 1890, p. 204.
M. lacunata Paetel, 1890, p. 205.
M. perviridis Paetel, 1890, p. 205.
M. muricata Saville-Kent, 1890*c*, p. 543; 1893, p. 215.
M. fucata Saville-Kent, 1897, p. 212; 1905, p. 3.
"Bastard pearl shell" Pace, 1899, p. 11.
Avicula (*Meleagrina*) *fucata* Collett, 1900, p. 2.
Pteria (*Margaritifera*) *vulgaris* Jameson, 1901, p. 384. Thiele, 1930, p. 590.
P. (*M.*) *lacunata* Jameson, 1901, p. 392.
P. muricata Hedley, 1910, p. 344.
Meleagrina lucunata Hedley, 1910, p. 344.
Pinctada vulgaris Hedley, 1916, p. 156; 1917, p. M7. Hynd, 1950, p. 69.
P. panasesae Allan, 1950, p. 267, fig. 64.
P. lacunata Iredale, 1939, p. 339.
P. aerata Iredale, 1939, p. 339.
P. perviridis Iredale, 1939, p. 340. Allan, 1946, p. 81; 1950, p. 267, fig. 64.

(*b*) *Discussion*

This Australian species is conspecific with the lingah pearl oyster of the East Indies and Persian Gulf. For this species Jameson (1901,

p. 384) used the name *vulgaris* Schumacher, remarking that this "must replace the more familiar *fucata* (Gould)".

Schumacher (1817, p. 108) quoted an earlier figure (Chemnitz 1785, Plate 80, Fig. 717) as being an illustration of his species *Perlamater vulgaris*. From an examination of Chemnitz's "synonymy" it is evident that he was confusing at least four species of pearl-shell. The specimen figured is obviously a lingah and is more like the East Indian than the West Indian species but there is no indication in the text of the origin of the specimen. However, the identity of Chemnitz's material is of no importance since Schumacher's own figure and description are the criteria on which the species *Perlamater vulgaris* is based. It has to be decided whether Schumacher's species is recognizable. Jameson (1901) is of the opinion that it is, and lists four characters which indicate that it is the Eastern lingah. (Schumacher gave no type locality.) His decision has apparently been accepted by subsequent authors with the exception of Iredale (1939, p. 335). The present author is of the opinion that Schumacher's figure is too poor and his description too brief to be of any real value and, in the absence of a type specimen and a type locality, regards the species as unidentifiable.

Avicula fucata Gould was described by Gould (1850, p. 309) from "Feejee?". In the same paper he described a species *A. lurida* from New Zealand. In a later paper (Gould 1852) he rearranged the names, type localities, and Latin and English descriptions of these species. As there is no evidence of intentional correction in Gould (1852) the names and descriptions appearing in Gould (1850) must stand. The type specimens are figured in Plate 5. Plate 5, Figure 2, shows the specimen described by Gould (1850) as *Avicula fucata* and figured in Gould (1852) as *Avicula lurida*. This specimen must therefore be accepted as the type specimen of *Avicula fucata* Gould. Plate 5, Figure 3, shows the type specimen of *Avicula lurida* Gould. In the author's opinion these specimens are conspecific and since *fucata* has page priority the name *Pinctada fucata* (Gould) must stand for the present species.

Reeve (1857) applied the names *perviridis, lacunata,* and *aerata* to special forms of this species. Reeve's illustration of *A. lacunata* shows a fairly young specimen which has apparently grown under good conditions as a result of which the growth processes are very well developed. *A. perviridis* and *A. aerata* are the green and bronze-yellow colour varieties. In everything except colour these two varieties agree closely with typical specimens of *P. fucata,* even to the transverse markings of the growth processes which are visible in Reeve's illustrations. Both colour varieties are of moderately frequent occurrence. Reeve's three species were catalogued by Paetel (1890).

Saville-Kent (1890*c*) applied *Meleagrina muricata* to a species of pearl oyster occurring in company with "the young of *Meleagrina margaritifera* (the commercial pearl shell) and the young of the smaller black lipped species here distinguished by the title of *Meleagrina nigromarginata*" on the under side of a hulk in Thursday I. harbour. Pace (1899, p. 11) has already noted that the "young of *Meleagrina margaritifera*" referred to by Saville-Kent were not the young of the commercial pearl-shell but a different species herein identified with *P. a. sugillata.* In the author's experience also *P. maxima* does not settle in such situations. The "smaller black lipped species here distinguished by the title of *M. nigromarginata*" has already been shown to be *P. margaritifera.* Again in the author's experience *P. fucata* is the only other species occurring in that particular environment. Thus *Meleagrina muricata* Saville-Kent becomes a synonym of *P. fucata* (Gould).

Saville-Kent (1897, p. 212; 1905, p. 3) applied *Meleagrina fucata* to Australian representatives of the lingah pearl-shell from Shark Bay and Torres Strait. Collett (1900, p. 2) also used the name *fucata* for "the pearl oyster of the Gulf of Manaar which also occurs in the Torres Strait".

Pace (1899, p. 11) did not use any specific name for the "bastard" shell of Torres Strait but he believed it "to be identical with that which is fished . . . mainly for the sake of its pearls — in Ceylon, the Persian Gulf, etc.".

Jameson (1901, p. 392) included *Avicula lacunata* Reeve in his list of species of uncertain position. Hedley listed *Pteria muricata* and *Meleagrina lacunata* from Queensland (1910, p. 344) and *Pinctada vulgaris* from Western Australia (1916, p. 156) and New South Wales (1917, p. M7). Presumably these records of Hedley's are all based on the earlier records of other authors. Thiele (1930, p. 590) recorded *Pteria vulgaris* from Shark Bay on the basis of one specimen collected by Michaelson and Hartmeyer.

Iredale (1939) prefers to regard *vulgaris* Schumacher as a synonym of *radiata* Leech and uses Reeve's three names *lacunata, perviridis,* and *aerata* to describe Queensland material. The author has examined Iredale's material in the Australian Museum collection and finds that his *P. aerata* and *P. perviridis* are in fact *P. fucata.* The specimens of *P. lacunata* referred to by Iredale (loc. cit., p. 339) could not be located but from the description it is evident that the species is synonymous with *P. fucata.*

Pinctada perviridis Allan (1946, 1950) and *P. panasesae* Allan (1950) are also synonymous with *P. fucata* (see also under *P. maculata*).

(*c*) *Description*

(i) *Form of Shell.*—In the spat and young specimens up to 1 month old the shell is very oblique and the ratio D.V.M.: hinge line = approx. 0.7, as in the specimens figured in Plate 4, Figure 1. As growth proceeds the shell becomes more erect but even in aged specimens the major axis is still slightly oblique, as in the specimen figured in Plate 4, Figure 2. In specimens about 6 months old D.V.M.: hinge line = approx. 1.0, but in older specimens this ratio is usually greater than 1.

(ii) *Anterior Border.*—In young specimens the anterior non-nacreous border lies wholly behind the reference line. With assumption of the more erect shell form, the non-nacreous border and a small part of the nacre come to lie in front of the reference line.

(iii) *Anterior Ear and Byssal Notch.*—The anterior ear is larger relative to shell size than in all other species. The ear of the right side is deeper than long. Typically the ears are straight but in occasional specimens they may be twisted slightly to the right.

The byssal notch never widens transversely as in *P. margaritifera* and *P. a. sugillata* but remains slit-like throughout life.

(iv) *Posterior Border.*—Typically the posterior border shows a slight to moderate sinus throughout life and a corresponding ear as in the specimen figured in Plate 1, but in many specimens the sinus is absent. The angle at which the posterior border meets the hinge line varies from acute to obtuse.

(v) *Convexity.*—This is the most convex of all the species. Young specimens are only moderately convex but there is a progressive increase in the ratio thickness: D.V.M. with age. In a collection of very old specimens from Scharapa Passage, Groote Eylandt, Gulf of Carpentaria, the average ratio was 0.44, with a maximum of 0.5.

(vi) *Growth Processes.*—Typically the growth processes are relatively small, tapering structures with finely rounded tips, flat at their base, but concave in section throughout the rest of their length. They may occur discretely or project from the edge of a continuous lamina. They usually lie flat on the shell but in rapidly growing specimens they may project outwards from their base and curve strongly downwards and inwards towards the tip. Typically they are arranged in radial rows but this arrangement is frequently obscured. Plate 1 shows a specimen in which the growth processes are characteristic.

Except in a very few instances they bear evenly spaced transverse markings which are extremely characteristic, and if present are absolutely diagnostic of the species. These markings are clearly visible in the specimen figured in Plate 1.

(vii) *Hinge Teeth.*—In young specimens the hinge teeth are always well developed. The anterior tooth of the left valve is usually above and slightly in advance of that of the right valve. In some specimens this tooth appears to be indented on its crown, in others it appears as 2 closely set cusps. The posterior tooth of the left valve is usually above that of the right valve. The right posterior tooth sometimes shows an accessory (dorsal) ridge. Plate 1 shows a young specimen in which both anterior and posterior hinge teeth are prominent.

In old specimens the hinge teeth tend to become more rounded and less prominent but are nearly always discernible.

(viii) *External Colour and Markings.*—This species exhibits 3 main external colour patterns. The commonest and that usually regarded as typical of the species consists of a series of well-defined continuous rays. The 2nd consists of small, more or less regularly dispersed flecks of colour while in the 3rd the colour is distributed evenly over the surface with sometimes a slight deepening of tint in the region of the reference axis. Many gradations between these 3 main types occur. The pattern is not always constant in the 1 specimen and occasional specimens may be found in which 2 or even all 3 of the main patterns have been assumed at different times. Such specimens are illustrated in Plate 5, Figure 1.

The colours most commonly occurring are reds and browns but spectacular colour varieties of green and bronze are frequently found. Pale cream, almost white, monochrome specimens also occur.

(ix) *Colour of Nacre and Internal Margin.*—In adult specimens the nacre is usually of a hard metallic lustre, particularly near the distal border. In old specimens a faint diffusion of yellowish green colour through the nacre may appear.

The non-nacreous border may be pale and transparent or bear 4 or 5 dark brown or red blotches corresponding to the main external rays. In older specimens these blotches invariably fuse to give a continuous dark lip to the shell.

(x) *Size.*—The largest specimen observed by the author measured 9 cm D.V.M. and 1.0 cm heel depth.

(*d*) *Distribution*

Jameson (1901, p. 386) states that in Australian waters this species ranges throughout north Australia, southward to Shark Bay in the west and Sydney in the east. The southern limits of this range have not been extended by subsequent authors. However, there are two specimens (C47238 and C50308) in the Australian Museum collection from "Victoria" and Mallacoota, Vic., respectively. The eastern range is therefore extended to northern Victorian waters.

The species occurs in company with *P. a. sugillata* from just above low water springs down to at least 12 fm. Large beds have been located off Groote Eylandt in the Gulf of Carpentaria at 12 fm resembling the famous beds of the Gulf of Manaar described by Herdman (1903). Extensive beds also occur in Moreton Bay but here the species occupies "grassy" intertidal banks situated just above low water springs.

PINCTADA MACULATA (Gould)

Plate 6, Figs. 1, 2; Plate 7, Figs. 1, 2

(*a*) *Synonymy*

Avicula maculata Gould, 1850, p. 309.

A. pica Gould, 1852, p. 443, pl. 39, fig. 549. Reeve, 1857, pl. 17, fig. 71 (non *A. pica* Philippi (1849)).

Avicula (*Meleagrina*) *pica* Dunker, 1872, p. 54, pl. 18, fig. 7.

Pteria (*Margaritifera*) *pitcairnensis* Jameson, 1901, p. 388 (nom. nov. for *A. pica* Reeve non Gould).

P. (*M.*) *panasesae* Jameson, 1901, p. 390, fig. 94 (nom. nov. for *A. pica* Gould non Reeve).

Margaritifera panasesae Allen, 1906, p. 410.

Pinctada panasesae Iredale, 1939, p. 336.

(*b*) *Discussion*

Gould (1850, p. 309) described a species *Avicula maculata* which he later appeared to rename *A. pica* (Gould 1852, p. 444) because the earlier name was preoccupied. However, perusal of Sherborn's "Index Animalium" and all available literature reveals no preoccupying name. In explanation of this discrepancy Mr. Joseph P. Morrison, Associate Curator, Division of Mollusks of the United States National Museum, has suggested (personal communication) that the plates and/or manuscript of the United States Exploring Expedition may have been printed but not published at the time Gould's 1850 paper appeared and that *maculata* Gould 1850 is a replacement of *pica* Gould (in press) preoccupied by *pica* Philippi 1849. Whatever the true explanation *maculata* Gould stands as the earliest available name for the present species.

Conrad (1837, p. 246) described two species *Avicula pallida* and *A. nebulosa* from the Sandwich Is. *A. pallida* has not been recorded since and Jameson (1901, p. 386) regarded it as synonymous with *A. nebulosa*, presumably as a juvenile. From the descriptions, *A. pallida* Conrad and *A. radula* Reeve (1857, Plate 8, Fig. 23) appear to be synonymous and there is a strong possibility that they may both be synonymous with *A. maculata* Gould, since certain young Barrier Reef specimens of *Pinctada maculata* exhibit the characteristic yellow and white colour described for *A. pallida* and *A. radula*. In addition Conrad (loc. cit.) says of *A. nebulosa* "epidermis with lamelliform serrated concentric wrinkles, the points of the wrinkles white, and disposed in the form of rays". This white colouring of the growth processes is characteristic of *Pinctada maculata* and supports the supposition that *A. pallida* Conrad is the young of *A. nebulosa* Conrad, and that both are synonymous with *A. maculata* Gould and *A. radula* Reeve. If this is so then *pallida* Conrad must replace *maculata* Gould for the present species. However, this could not be rigidly proved without examination of the types of *A. pallida* and *A. nebulosa* which according to Dall, Bartsch, and Rehder (1938, p. 73) are lost, and of the type of *A. radula* Reeve which is presumably in the British Museum. Accordingly *maculata* Gould is retained for the species.

A. nebulosa auct. non Conrad may or may not be synonymous with *A. maculata* Gould but it is significant that Reeve (1857) says of his species — "remarkable for the rich delicate golden hue of its internal nacre", a feature characteristic of *Pinctada maculata*.

Jameson (1901, p. 390) substituted the name *Margaritifera panasesae* for *A. pica* Gould 1852 which was preoccupied by *A. pica* Philippi 1849. He preferred to regard *A. pica* Reeve as distinct from *A. pica* Gould and gave it the name *M. pitcairnensis* (loc. cit., p. 388). However, his re-description of the species from the type does not include any important character which would separate *M. pitcairnensis* from *M. panasesae,* so both his names fall into the synonymy of *Pinctada maculata.*

Allen (1906, p. 410) discussed the biology of *M. panasesae* in its type locality, the Conflict Group, New Guinea. Iredale (1939, p. 336) referred to *P. panasesae* all "small adult convex pearl shells found along the Barrier Reef" remarking that "this is the species most commonly regarded as '*vulgaris* Schumacher' ". The author has examined material from the Capricorn Group, Barrier Reef, in the Australian Museum collection labelled *P. panasesae* by Iredale. This consists of a collection of seven stunted, deformed, and water-worn valves which do in fact belong to *M. panasesae* Jameson (= *maculata* Gould) and a single larger right valve belonging to *P. a. sugillata* (Reeve). Allan (1950, p. 267) adopted Iredale's definition but her illustration is of a typical example of well-grown *P. fucata.*

This species has also been discussed by Seurat under the name *Margaritifera panasesae* in a series of papers dealing with the biology of the species in the Tuamotu Archipelago (Seurat 1904*a*; 1904*b*; 1904*c*; 1904*d*; 1906).

(*c*) *Description*

(i) *Form of Shell.*—In the form of the shell this species rather resembles *P. fucata* except that in the adults the shell is slightly more erect. The young are oblique (as evidenced by the specimens figured in Plate 6, Fig. 1) but the obliquity decreases with age until in the adult the shell is erect or slightly oblique, rarely obtuse.

As in *P. fucata* the ratio D.V.M.: hinge line = approx. 1 in young specimens, exceeds 1 in adults.

(ii) *Anterior Border.*—Again as in *P. fucata* the anterior border lies behind the reference line in very young specimens, in advance of it in adults. The area of nacre in advance of the line is slightly greater than in *P. fucata.*

(iii) *Anterior Ear and Byssal Notch.*—The anterior ear is moderate to large in size. The ear of the left side extends well in advance of that of the right side in young specimens, less so in adults.

The byssal notch is slit-like in juveniles but usually broad transversely in the adult.

(iv) *Posterior Border.*—Typically there is a slight posterior sinus and a small ear as in *P. fucata.* However, the sinus is frequently absent, in which case the posterior border may be straight or convex.

(v) *Convexity.*—The shell as a whole is convex, approaching the condition found in *P. fucata*. In old, dwarfed specimens such as are found on the Barrier Reef this condition is enhanced and the left valve is strongly convex, the right valve slightly to moderately convex.

(vi) *Growth Processes.*—As in *P. fucata* the growth processes are typically slender, tapering structures, with finely rounded tips. They are usually concave in section, sometimes flat, and are slightly curved throughout their length. They are usually discretely arranged but sometimes project from the edge of a raised lamina. In most specimens they lie fairly close to the shell. Characteristically they are opaque white in colour, sometimes horny, and never show the transverse dark and light bands characteristic of *P. fucata*. Typically they are arranged in radial rows though this arrangement is often obscured. They are relatively small and numerous as in *P. fucata*. Plate 6, Figure 2, shows a specimen in which more or less typical growth processes occur.

(vii) *Hinge Teeth.*—The hinge teeth have practically the same structure and arrangement as in *P. fucata* with the exception that the posterior pair are more strongly developed and both pairs are rarely obscured in adult specimens.

The anterior pair are small, more or less conical projections, that of the left side sometimes being indented on the crown, or even double. That of the right side is usually simple and lies slightly below that of the left side.

The posterior pair take the form of heavy ridges starting on the hinge line just in advance of the posterior end of the ligament and curving backwards and downwards onto the surface of the nacre. That of the right side is more strongly developed than that of the left side and is situated slightly lower down. Parallel accessory ridges may develop on either or both valves so that the teeth appear double. When both members of the pair are double, the ridges interlock. Both members of the pair are strongly developed and appear sometimes to increase in prominence with age.

In his original description Gould (1850, p. 309) stated that the lateral (posterior) tooth is bifurcate in the right valve but in his (1852, p. 443) description he stated that it is the left member of the pair which is bifurcate and shows it in his illustration. Jameson (1901, p. 390) merely remarks that the teeth are as in *M. vulgaris*.

(viii) *External Colour and Markings.*—According to Gould (1850) the external colour pattern together with the colour of the nacre and the colour of the internal non-nacreous margin make the appearance of this species very distinctive. He describes the external surface as "magnesian radiated with dark purple". Jameson (1901, p. 391) records the external colour as "white with 6 to 10 green, brown or black radii, which are very variable in some cases being almost entirely suppressed in others being confluent so that the shell is a uniform dark colour". Plate 7 shows Gould's and Jameson's type specimens. The characteristic patterns are clearly visible.

The specimens in the Australian Museum show a variety of patterns and colours in which the presence of porcellanous white patches, rays, or flecks constitutes the nearest approach to a constant character. Even this is absent in some small specimens. The colours and patterns range from a pale monochrome through pale to bright yellow monochrome to a rayed or blotched pattern involving usually the porcellanous white and purples, browns, or greens. Occasional dark monochrome specimens are seen.

A finer, superimposed pattern of thin, wavy or zig-zag, more or less parallel, red-brown lines may sometimes be observed. This pattern is not to be confused with the transverse bands of the growth processes (including their basal parts) of other species.

(ix) *Colour of Nacre and Internal Margin.*—A characteristic feature of the species is the appearance of a pale yellow to deep orange colour in the nacre proper. This colour, as in other species, appears to deepen with age. It is sometimes absent even in old specimens.

Gould (1852, p. 443) describes the internal non-nacreous margin as "variegated blue-black and porcelain-white". Jameson (1901, p. 391) describes it as "white with dark purple blotches corresponding to the radial bands". These features are clearly visible in the type specimens shown in Plate 7, Figures 1 and 2. From the material in the Australian Museum it seems that the presence of white porcellanous patches on the margin is characteristic of the species. However, these patches are frequently absent in young specimens, the margins being clear and horny. In many of the older specimens the margins are exactly as described by Gould and Jameson with the exception that the darker blotches frequently do not coincide with the external rays. Analysis of the colour patterns of the margins shows that, while there is sometimes in the extreme distal portion a radial pattern of dark patches corresponding to the external rays, in the portion immediately distal to the nacre there is usually a circularly disposed dark band somewhat irregular in form and frequently broken up into more or less discrete patches. In the progress of growth these bands are repeated at intervals, producing a series of concentric dark rings which gradually become overlaid with nacre. In young specimens in which the nacre is still fairly thin and transparent the rings are still visible and lend a characteristic appearance to the nacre. These rings can be made out in Jameson's type specimen figured in Plate 7, Figure 2.

(x) *Size.*—The largest specimen in the Australian Museum collection measures 5.5 cm D.V.M. and 0.4 cm heel depth. However, nearly all the specimens appear to have grown in shallow water under slightly unfavourable conditions and it is to be expected that the maximum size of this species would be rather larger. Seurat (1906, p. 25) gives the maximum size as 5.0 cm.

Iredale (1939) regards the "crass" growth of his specimens relative to their size as characteristic of the species. The condition appears to be characteristic of the Australian Barrier Reef specimens examined but is probably the result of unfavourable environmental conditions.

(*d*) *Distribution*

This species appears to have a distribution extending from the central Pacific across to the west and into the Indian Ocean. The most easterly record is that of Reeve (1857) from Pitcairn I. Northward of the equator the species occurs at Palmyra I. (Aust. Mus. C61074 — 2 juv.) and Loo Choo Is. (Jameson 1901). Southward the species extends to the Kermadec Is. (Aust. Mus. C36622 — 3 spec.), Norfolk I. (Aust. Mus. C59876 — 2 spec.), and Lord Howe I. (Aust. Mus. C2829 — 7 spec., C6884 — 1 spec., C59606 — 5 spec., and Jameson (loc. cit.)). The species is recorded from the Tuamotu Archipelago by Seurat (1904*a*; and later papers), from Fiji and Samoa by Jameson (loc. cit.), and there are specimens in the Australian Museum from Marutea (C17561 — 2 spec.), Mangareva (C17196 — 1 spec.), Lagon de Tiaro (C61648 — 1 spec.), Reef I., Santa Crux Group (C52138 — 11 juv.), Tonga Tabu (C37666 — 1 juv.) New Caledonia (C55392 — 1 spec.), New Britain (C45639 — 3 juv.), and New Hanover (C45975 — 4 juv.). In the New Guinea area Jameson (loc. cit.) records the species from the Conflict Group, Bonvouloir Group, Samarai, and Moresby. There is also one specimen in the Australian Museum (C61654) from Aroma near Port Moresby. In the Australian area proper the species is recorded from Badu I., Torres Strait, and "Australia" (Jameson, loc. cit.) and the Great Barrier Reef (Iredale 1939). The only material in the Australian Museum labelled *P. panasesae* by Iredale is the collection (C59135 — 7 spec.) from the Capricorn Group referred to earlier. There is additional unlabelled material from the Capricorn Group (C58364 — 8 juv.), Lizard Group (C41814 — 2 valves), St. Crispin Reef (C61655 — many juv.), Michaelmas Cay (C61656 — many juv.), Ballina, N.S.W. (C61647 — 1 spec.), Yamba, Clarence R., N.S.W. (C61657 — 5 juv.), and Shellharbour, N.S.W. (C50242 — 4 juv.). The author has also seen one specimen from Double I., near Cairns, north Qld. The only record for the Indian Ocean is that of Jameson (loc. cit.) from Cocos-Keeling Is. He also records "? distinct" specimens of the species from South Africa.

As far as the Australian distribution is concerned the species appears to occur only on the east coast from Torres Strait to southern New South Wales.

The species has been recorded only from shallow water. Jameson found it in rock pools and on reef flats. Seurat (1904*a*, 1904*c*, 1905, 1906) records it from the lagoons of the Tuamotu Archipelago where apparently it is found on the reef flats and on *P. margaritifera* from banks in 4-5 m. All the material of this species in the Australian Museum collection is either from the lower intertidal zone or just below.

PINCTADA CHEMNITZI (Philippi)

Plate 8, Figs. 1, 2; Plate 9, Figs. 1, 2

(*a*) *Synonymy*

"Die glatte dunnschalichte gestrahlte perlenmuttermuschel" Chemnitz, 1785, p. 135, pl. 80, fig. 720.

Avicula atlantica var. *b* Lamarck, 1819, p. 149.

A. atlantica Lam 8 var. Desh. Pfeiffer, 1840, p. 76.

A. Chemnitzii Philippi, 1849, p. 19.

A. tegulata Reeve, 1857, pl. 7, sp. 17; 1860, p. 64 (non *A. tegulata* Goldfuss (1836)).

A. (*Meleagrina*) *Chemnitzii* Dunker, 1872, p. 15, pl. 3, fig. 5.

Meleagrina tegulata Paetel, 1890, p. 206. Melvill and Standen, 1899, p. 184. Hedley, 1910, p. 344.

Pteria (*Margaritifera*) *tegulata* Jameson, 1901, p. 392.

P.(*M.*) *chemnitzii* Jameson, 1901, p. 388.

Pinctada epitheca Iredale, 1939, p. 336, pl. 5, figs. 14, 14*a* (nom. nov. for *A. tegulata* Reeve).

(*b*) *Discussion*

Philippi (1849, p. 19) recorded *Avicula Chemnitzii* from the China Sea, at the same time giving as a synonym "Die glatte dunnschalichte gestrahlte perlenmuttermuschel" of Chemnitz (1785, p. 135) which was from Tranquebar. Chemnitz's species had previously been referred by Lamarck (1819, p. 149) to *Avicula atlantica* var. *b* and under that name it was catalogued by Pfeiffer (1840, p. 76). Dunker (1872, p. 15) redescribed and figured Philippi's species, giving the locality as China Seas. It is not clear whether Dunker examined Chemnitz's or Philippi's material.

Avicula tegulata Reeve 1857 from Moreton Bay is synonymous with this species. Iredale (1939, p. 336) substituted *Pinctada epitheca* for *A. tegulata* Reeve which is preoccupied by *A. tegulata* Goldfuss (1836). Iredale's type specimen came from Townsville, Qld. It and other specimens from Australian waters possess a distinct posterior hinge tooth of characteristic form. Philippi (loc. cit.) makes no mention of the posterior tooth in his species but Dunker (loc. cit.) shows the tooth perfectly in his illustration. The radial ridges on the nacre and the marked difference in nacreous area of the two valves characteristic of Australian specimens are not shown in Dunker's figure but the outline of the valves agrees perfectly.

Paetel (1890, p. 206) catalogued Reeve's *tegulata*. Melvill and Standen (1899, p. 184) recorded *M. tegulata* from Torres Strait. Jameson (1901, p. 392) regarded *A. tegulata* Reeve as of uncertain standing. Hedley (1910, p. 344) listed *M. tegulata* for Queensland on the record of either Reeve or Melvill and Standen or both.

(*c*) *Description*

(i) *Form of Shell.*—In outline the shell rather resembles *P. fucata* except for the posterior ear region which is much more strongly developed.

The shell is also markedly inequivalve, the left valve being conspicuously larger than the right. The nacreous surface of the left valve is also conspicuously larger than that of the right. These features are amply illustrated in specimens figured in Plate 8, Figures 1 and 2.

In all specimens examined the shell was moderately oblique, growth rings and coloured rays indicating that there was a decrease in obliquity with age. The reference axis appears never to become vertical.

(ii) *Anterior Border.*—Both the nacreous and non-nacreous anterior borders lie in advance of the reference line. Iredale (1939, p. 336) states that "the rostrum is also so repressed that the anterior side of the left valve shows no sinuosity". Examination of his type specimen figured here in Plate 9, Figure 2, reveals that such is the case only because the specimen is damaged and half the rostrum (or ear) is missing. In all other specimens examined there is a pronounced sinus and moderate-sized ear.

(iii) *Anterior Ear and Byssal Notch.*—As just noted the anterior ear is moderately well developed, the left being slightly larger than the right. The right ear differs from that of other species in that it is usually longer than deep and the anterior end is broadly rounded. The byssal notch remains slit-like throughout life as in *P. fucata.*

(iv) *Posterior Ear.*—A long hinge line, deep posterior sinus, and correspondingly large posterior ear are characteristic of this species. These features may be made out in the specimens figured in Plate 8, Figures 1 and 2, and Plate 9, Figure 1. However, in a few specimens seen, the ear was not well developed and approximated to the condition found in *P. fucata.*

(v) *Convexity.*—The species is strongly convex, approaching the condition found in *P. fucata.* Iredale (1939, p. 336) states that the right valve is comparatively flat. This valve is now missing from his type specimen but in another specimen of comparable size the right valve is present and is as Iredale states. In older specimens, however, the right valve is rather more convex. The convexity of the shell as a whole appears to increase with age.

(vi) *Growth Processes.*—In the few specimens examined in which the growth processes remain, these appear as broad, parallel-sided structures with rounded ends. They resemble those of *P. a. sugillata* except that they are slightly longer for their width and more sparsely distributed, not projecting from the edge of a raised lamina. In section they are flat or concave and are arranged in radial rows. In colour they usually resemble the basic external colour of the shell but frequently they bear parallel, curved, transverse bands of a white or pink colour. These processes can be seen in the specimen figured in Plate 8, Figure 2.

Jameson (1901) includes *M. chemnitzii* in his Section *c* with the typical lingah pearl oysters. In shell form and convexity this species approaches the lingahs but in the nature of the growth processes it shows a relationship to Jameson's Section *b*, the "*sugillata*" group of species.

(vii) *Hinge Teeth.*—The hinge teeth are well developed but are unusual in that the posterior pair are more strongly developed than the anterior pair. The posterior pair occupy the normal position on the shell except that in a few specimens they start well in advance of the posterior end of the hinge ligament. The ridge is well defined and in most older specimens cuts off a small flat facet of the nacreous surface which has a characteristic appearance as in the specimens figured in Plate 8, Figures 1 and 2. The anterior pair are simple rounded or oval projections, not as strongly developed as the posterior pair and sometimes almost obscured.

Insufficient material has been examined to determine whether there are any changes with age except that the posterior pair appear not to decrease, but perhaps increase, in size with age.

(viii) *External Colour and Markings.*—Iredale (1939, p. 336) gives the colour of his type specimen as "dull brownish indistinctly rayed with paler shades". On examination these rays were found to be formed by rows of discrete transverse, pale pink or white markings which obviously had been associated with the basal portions of growth processes. These markings can be seen in the specimens figured in Plate 9, Figures 1 and 2. Other specimens seen ranged from a deep red-brown rayed with faint dark brown rays to pale cream, again bearing the radial rows of transverse white markings. These radial rows correspond to the rows of growth processes. The paler-coloured shells appear to be the more numerous.

(ix) *Colour of Nacre and Internal Margin.*—The nacre has the hard metallic lustre of *P. fucata.* In one older specimen there was a faint perfusion of yellow colour through the nacre.

The internal non-nacreous margin varies from pale cream to dark red-brown, depending on the external coloration, and is without prominent patches or markings.

(x) *Surface of the Nacre.*—The nacreous surface in all specimens examined bears small radially arranged corrugations which are sufficiently prominent in some places to be detected by touch as well as sight. These corrugations can be made out in the shells shown in Plate 8, Figures 1 and 2. They also occur occasionally in other species, particularly *P. fucata,* but are never as prominent. They may be regarded, along with the inequality of the valves, the shape of the posterior ear, and the posterior hinge teeth, as one of the more important diagnostic characters.

(xi) *Size.*—The largest specimen examined had a D.V.M. of 9.5 cm, A.P.M. of 8.5 cm, and hinge line of 9.5 cm. The oldest specimen seen had a heel depth of 0.6 cm.

It is to be expected that the maximum size of this species is larger than that of *P. fucata,* possibly as large as that of *P. a. sugillata.*

(*d*) *Distribution*

Reeve (1857) gives the type locality of *A. tegulata* as Moreton Bay but Iredale (personal communication) is of the opinion that the name

"Moreton Bay" probably refers not so much to the bay itself as to the penal settlement established there and that the actual locality for the shell may be anywhere from Moreton Bay northwards.

Iredale's type (Aust. Mus. — C60343) came from Townsville. There are further specimens in the Australian Museum from Cardwell (C61653 — 1 spec.), Keppel Bay (C58514 — 1 spec.), and Yirrkala, near Cape Arnhem, N.T. (C61344 — 1 right valve, 1 complete specimen). There is also one specimen in the Queensland Museum (7700) from Townsville and a second unlocalized specimen. Recently the F.R.V. *Gahleru* has collected the following material from the Cape York and Gulf of Carpentaria area: Escape River, Cape York Peninsula, 1 specimen, from river mouth, depth 6 fm; station 15 miles NE. of Carpentaria Lightship, Torres Strait, 1 specimen, depth 16 fm; Cape York Peninsula at Crab I., 5 specimens, from mainland coastal reef; Cape York Peninsula at Mapoon, 1 specimen, from mainland coastal reef; Groote Eylandt, Gulf of Carpentaria, 10 specimens, off western coast of the island, depth 8-10 fm.

Outside Australian waters the species has been recorded from Hongkong and various localities in the Indian Ocean by Prashad and Bhaduri (1933), Tranquebar by Chemnitz (1785), Sumba and Sumbawa by Prashad (1932), Philippines by Reeve (1857) (as *A. praetexta*), China Sea by Philippi (1849), and Japan by Habe (1951).

There are no records of the depth at which specimens were taken except for those collected by the F.R.V. *Gahleru*. From this material it appears that the depth range is at least 0-16 fm. Prashad's (loc. cit.) specimens were taken between 0 and 15 fm.

PINCTADA ALBINA (Lamarck)

Plate 12, Figs. 2, 3

(*a*) *Synonymy*

Meleagrina albina Lamarck, 1819, p. 152.
Avicula albina Deshayes, 1830, p. 102.

(*b*) *Discussion*

Meleagrina albina Lamarck was originally described from "les mers de la Nouvelle Hollande, au canal d'Entrecasteaux et à la terre de Diemen". Lamy (1935, p. 133) re-examined Lamarck's material and found two boxes of specimens, one containing two specimens from "Oceanie", the other marked "var. *b*" containing a single specimen from "Nouvelle-Hollande". The author's colleague, Mr. J. M. Thomson, has also examined Lamarck's types and finds that the localities are as stated by Lamy. The "Oceanie" of Lamarck may include the whole of the Indo-Pacific area since the term is used in that sense by contemporary French authors. The specimens are not marked as having been collected by Peron and there is no other indication of locality.

Prashad (1932, p. 99) regarded *albina* Lamarck as a synonym of *vulgaris* Schumacher while Iredale (1939, p. 336) suggested that "*M. albina* is probably founded on a Sharks Bay shell, the species we now call *carchariarum* Jameson". Thomson (personal communication) has furnished notes on several of the more important specific characters and these, in combination with the photographs reproduced in Plate 12, Figures 2 and 3, enable the author to state that the larger of Lamarck's types (Plate 12, Fig. 2) is conspecific with the Australian species hitherto known as *P. sugillata* (Reeve) and *P. carchariarum* (Jameson).

In this specimen the growth processes have almost all been eroded or damaged but enough of them remain to show them to have been broad structures closely packed towards the edge of the shell. The anterior ear is small, the byssal notch broad, hinge teeth are not visible, and the anterior border projects well in advance of the reference line. Thomson describes the nacre as "washy yellow", the non-nacreous border as "off white, with no trace of dark pigment", and the external surface as "white, possibly sunbleached". The specimen appears to be about the same age as that figured in Plate 12, Figure 1. The most obvious difference lies in the colours of the non-nacreous borders and external surfaces, characters which are of major diagnostic importance in separating the two subspecies *P. a. sugillata* and *P. a. carchariarum* to be described later. Lamarck's specimen tends towards the condition typical for *P. a. carchariarum* but the range of variation of both subspecies is such that the specimen could belong in either.

Lamarck's smaller specimen (Plate 12, Fig. 3) may be conspecific with the larger but it is impossible to be sure without examining it personally. To eliminate the possibility of future confusion the author selects the larger of Lamarck's specimens as the holotype.

As there is no definite type locality for *Meleagrina albina* Lamarck and as the holotype lies within the range of variation of both subspecies, the author prefers not to associate it definitely with either subspecies but to record each subspecies under the next available name.

Lamarck's *M. albina* var. *b* is synonymous with *P. fucata* (Gould) the East Indian lingah. *Avicula albina* var. *Vaillanti* Vassel (1896, p. 465) and *Meleagrina albina* Giard (1903, p. 1244; 1904) are probably also synonymous with *P. fucata* (Gould).

PINCTADA ALBINA SUGILLATA (Reeve)

Plate 9, Fig. 3; Plate 10, Figs. 1-3; Plate 11, Figs. 1-3; Plate 12, Fig. 1; Plate 13, Fig. 2

(*a*) *Synonymy*

Avicula fimbriata Reeve, 1857, pl. 9, sp. 25. Whitelegge, 1889, p. 244 (non *A. fimbriata* Dunker (1852)).

A. sugillata Reeve, 1857, pl. 9, sp. 27.

A. irradians Reeve, 1857, pl. 10, sp. 35.
A. chamoides Reeve, 1857, pl. 11, sp. 41.
Margaritifera fimbriata Angas, 1867, p. 930. Henn and Brazier, 1894, p. 181.
Avicula (Meleagrina) Reeveana Dunker, 1872, p. 45, pl. 15, fig. 1 (nom. nov. for *A. fimbriata* Reeve).
Meleagrina irradians Paetel, 1890, p. 205.
M. Reeveana Paetel, 1890, p. 205.
M. sugillata Paetel, 1890, p. 206. Hedley, 1910, p. 344.
Pteria (Margaritifera) sugillata Jameson, 1901, p. 380.
Pinctada sugillata Hedley, 1916, p. 156. Iredale, 1939, p. 338. Allan, 1946, p. 81; 1950, p. 267, fig. 64. Hynd, 1950, p. 69.
P. perrutila Iredale, 1939, p. 337, pl. 5, fig. 15.
P. placunoides Iredale, 1939, p. 337.
P. irradians Iredale, 1939, p. 338.
P. reeveana Iredale, 1939, p. 338. Allan, 1950, p. 267, fig. 64.

(*b*) *Discussion*

Reeve (1857) described three species of pearl-shell from Australian waters, *A. fimbriata, A. sugillata,* and *A. irradians,* which were regarded by Jameson (1901, p. 380), who examined the types, as synonymous. Of the three, *A. fimbriata* has sequence priority but is preoccupied by *A. fimbriata* Dunker (1852), so that *A. sugillata* is the valid name. At the same time *A. Reeveana* Dunker 1872, erected by Dunker for *A. fimbriata* Reeve, becomes a synonym of *A. sugillata* Reeve. A further synonym is *A. chamoides* Reeve (1857) which was based on young specimens of *A. sugillata.*

Pinctada perrutila Iredale was erected for thin-shelled, purple coloured specimens which are here regarded as a colour variety of *P. a. sugillata. Avicula rutila* Reeve (1857, Plate 8, sp. 19) resembles Iredale's species closely and if examination of the type should prove it to be a *Pinctada* then *rutila* Reeve must take the place of *sugillata* Reeve for the present subspecies. In addition *A. atropurpurea* Dunker (1852, p. 76) resembles *A. rutila* Reeve and *P. perrutila* Iredale, and if examination of the type shows Dunker's species to be conspecific with the others then *atropurpurea* Dunker precedes both *rutila* Reeve and *sugillata* Reeve for the present subspecies.

Angas (1867) recorded *M. fimbriata* from Port Jackson and Whitelegge (1889) listed this record. Paetel (1890) listed *M. irradians, Reeveana,* and *sugillata* for Australia. Hedley (1910) listed *M. sugillata* for Queensland and (1916) *P. sugillata* for Western Australia. Iredale (1939) preferred to regard Reeve's species as distinct. He recorded *P. reeveana, P. sugillata, P. irradians,* and *P. placunoides,* all of which are regarded here as synonyms. His specimen of *P. reeveana* (Aust. Mus. C57345) from Port Darwin is a typical example of the obtuse form often assumed by *P. a. sugillata* growing on or under flat rock slabs in the lower intertidal zone. A single specimen (Aust. Mus. C12842) from Caloundra, identified by Iredale as *P. irradians,* is a typical erect specimen of *P. a.*

sugillata. It is interesting to note that the growth lines on this specimen show that at an earlier date the body form was much more obtuse than at the time the specimen was taken. A single specimen (Aust. Mus. C58355) from Port Curtis labelled *P. placunoides* by Iredale is a pale monochrome specimen of *P. a. sugillata.* This specimen was dredged on a muddy bottom and is quite typical of *P. a. sugillata* grown under such conditions.

The type specimen of *P. perrutila* Iredale from Nor-west It., Capricorn Group, cannot be located in the Australian Museum, nor can the "two smaller shells agreeing" from Low Is. However, there are four specimens in the collection (C43698 from Moreton Bay, C18787 from Gatcombe Head, C10068 from Palm Is., and C61652 from Low Is.) which Iredale (personal communication) regards as typical examples of his *P. perrutila.* All four specimens are examples of a reasonably common and distinctive colour form of *P. a. sugillata.* In this form the shell is usually monochrome, of a red, purple, dark brown, or even black colour, with sometimes faint traces of radial rays. The growth processes are often sparse or absent as is sometimes found in the white monochrome form of the same species. It is interesting to note that specimen C18787 figured in Plate 11, Figure 1, still retains the outer shell layer in the region of the umbo and it is evident that when very young this specimen was pale green in colour, rayed with white. The reverse change is evident in the specimen C61646 figured in Plate 11, Figure 2. In this specimen the colour in youth was deep red-brown and changed to a clear horny colour with a few small red-brown blotches.

(*c*) *Description*

(i) *Form of Shell.*—The spat of this species and specimens up to 1 month old are very oblique and the ratio D.V.M.: hinge line is approx. 0.7 as in *P. fucata.* This condition is clearly illustrated by the specimens figured in Plate 9, Figure 3. Again as in *P. fucata* the obliquity of the shell decreases with age until in old specimens the shell may be extremely obtuse. Specimens about 6 months old have a D.V.M.: hinge line ratio of approx. 1.0 while in old specimens this ratio may be as high as 2.0.

(ii) *Anterior Border.*—In young specimens the anterior non-nacreous border lies wholly behind the reference line. With decrease in the obliquity of the shell the border comes to extend well in advance of the reference line. This development is often exaggerated in specimens growing on or under flat rock slabs in the lower intertidal zone and specimens such as that figured in Plate 10, Figure 3, result. In normal adult specimens a small proportion of the nacre also projects in advance of the reference line.

(iii) *Anterior Ear and Byssal Notch.*—The anterior ear is smaller in this species than in any other.

The plane of the anterior ear of both valves invariably differs from that of the rest of the valve, being twisted so that the hinge line when viewed from above curves markedly to the right at its anterior end.

The byssal notch is narrow in young specimens but widens transversely with age so that in old specimens it gapes widely.

(iv) *Posterior Border.*—In very young specimens (up to 1 month old) the posterior border shows a slight sinus and a correspondingly small ear. As development proceeds this sinus may either disappear and the ear with it, or the sinus may deepen and the ear become increasingly prominent as in the specimen figured in Plate 10, Figure 1. Whatever the course followed in development, the hinge line eventually ceases to grow while the posteroventral border continues, and in old specimens the posterior border assumes a slightly sinuous outline with the angle between the posterior border and the hinge line very obtuse. This condition is demonstrated by the specimens figured in Plate 11, Figure 3, and Plate 12, Figure 1.

(v) *Convexity.*—The left valve is convex, the right valve flat to slightly convex in young specimens, moderately convex in old specimens.

The shell as a whole is moderately convex, the ratio thickness: D.V.M. never approaching the maximum value of 0.5 found in *P. fucata*.

(vi) *Growth Processes.*—The growth processes are typically broad, short, parallel-sided structures with blunt rounded ends. Occasionally they may be bluntly clavate or slightly tapered. In section they sometimes appear as described by Jameson (1901, p. 380) particularly in well-grown specimens, but more often they are simply concave. Normally they curve downwards and inwards in their distal half and the distal processes of each valve interdigitate.

In very young specimens (up to 1 month old) growth processes are absent or sparse and discrete. In juveniles they may be discrete or appear as projections from the distal edge of a continuous raised lamina. This usually occurs in specimens grown under optimum conditions, the concentric rows of processes appearing as regularly arranged "frills". In adults they are usually absent from the external surface of the shell except near the lip, where the consecutive rows are closely packed and the lip presents a rough thickened appearance.

Typically the processes are arranged in radial rows though this pattern is often obscured. The individual processes are sometimes the same tint as the external surface of the shell but more frequently they are opaque white or opaque white and dark alternately. Plate 9, Figure 3, and Plate 10, Figures 1-3, show specimens in which the growth processes are characteristic.

(vii) *Hinge Teeth.*—The hinge teeth have their strongest development in juveniles, becoming partially or completely obscured with age. In specimens up to 6 months old the anterior pair appear as small conical or rounded projections, that of the left side being in advance of or slightly below that of the right side. Of the posterior pair that of the left side is the larger and longer.

In the adult the posterior pair are usually completely obscured, while the anterior pair may remain as faintly discernible rounded humps.

(viii) *External Colour and Markings.*—The external surface of the valves can exhibit a range of colour and pattern varying from an even white or cream through a rayed or flecked black and white pattern to an even dark monochrome. In addition green, bronze, pink, dark red, and brown monochrome or rayed varieties may occasionally be seen.

Rayed patterns predominate in collections taken near low tide mark. The white or cream monochrome specimens are most frequently seen in collections taken from "deep" water (10 fm or more) or in culture cages where light is obscured and muddy conditions prevail. The other varieties make their appearance at random.

(ix) *Colour of Nacre and Internal Margin.*—In young specimens the nacre usually presents a hard metallic lustre, deepening to a darker tint at the distal border. In old specimens this dark tint tends to disappear and is sometimes replaced by a delicate suffusion of yellow over all or part of the nacre.

Typically the nacre is bounded by a narrow black band on the non-nacreous margin extending, in its greatest development, from the anterior to the posterior ear. This band may be present only in the middle third of the border, or broken up into discrete patches, or even completely absent. In some specimens a thin deposit of white pigment may be seen outside the black band, rendering it even more prominent. Plate 10, Figure 3, shows a specimen in which the black band is moderately well developed.

(x) *Size.*—The largest specimen seen by the author measured 11 cm D.V.M. and 1.0 cm heel depth.

(*d*) *Distribution*

The subspecies has been recorded from north-west Australia (*A. fimbriata* Reeve 1857); Port Essington, N.T.; Torres Strait; Cape Hillsborough, Qld (*P. sugillata* Jameson 1901); Port Darwin; various Queensland localities (*Pinctada* spp., Iredale 1939); Port Jackson (*M. fimbriata* Angas 1867). There is material in the Australian Museum collection ranging from Port Darwin (C11835 — 1 spec.; C57345 — 1 spec.) to Shell Harbour, N.S.W. (C61651 — 1 spec.). The author has also examined much material from the Groote Eylandt area, Torres Strait, and Moreton Bay collected during the course of these investigations.

The eastern limit of the Australian range is therefore southern New South Wales. The western limit is ill-defined. Between Port Darwin and Shark Bay, *P. a. sugillata* is replaced by *P. a. carchariarum* (for further discussion see under *P. a. carchariarum*).

Outside Australia the subspecies has been recorded under the name of *P. sugillata* by Prashad (1932, p. 101) from various localities in the

East Indies and by Herasawa (1937, p. 150) from the Celebes. It is probable that it has also been recorded under other names.

The subspecies usually occurs along with *P. fucata* from just above low water springs down to at least 22 fm. It thrives particularly well on "grassy" intertidal banks which emerge on the low spring tides and is found in large numbers in Moreton Bay and at Groote Eylandt under these conditions. Plate 13, Figure 1, shows a portion of a grassy intertidal bank in Scharapa Passage, Groote Eylandt. Plate 13, Figure 2, is a close-up of portion of the same bank showing the heavy growth of *P. a. sugillata.*

PINCTADA ALBINA CARCHARIARUM (Jameson)

(*a*) *Synonymy*

Avicula margaritifera Griffin, 1886, p. 434.
Meleagrina imbricata Saville-Kent, 1897, p. 209. Seurat, 1905, p. 132.
Avicula (*Meleagrina*) *imbricata* Collett, 1900, p. 2.
Pteria (*Margaritifera*) *carchariarum* Jameson, 1901, p. 381, fig. 92. Thiele, 1930, p. 590.
Pinctada carchariarum Hedley, 1916, p. 155; 1924, p. 6. Hynd, 1950, p. 69. Allan, 1950, p. 266, fig. 64.

(*b*) *Discussion*

Jameson (1901) applied the name *M. carchariarum* to the Shark Bay shell of commerce. Previously the species had been recorded as *A. margaritifera* by Griffin (1886) and *M. imbricata* by Saville-Kent (1897) and Collett (1900). Seurat (1905) persisted in the use of *imbricata* for the Shark Bay shell. Hedley (1916, 1924), Hynd (1950), and Allan (1950) employed *P. carchariarum.*

(*c*) *Description*

The author considers it unnecessary to give a complete formal description. Instead the differential characters only are listed.

Jameson (loc. cit.) noted the following differences between *P. carchariarum* and *P. sugillata*:

(i) *P. sugillata* is more convex than *P. carchariarum.*

(ii) The hinge is relatively shorter in *P. sugillata* than in *P. carchariarum.*

(iii) The posterior border of *P. carchariarum* meets the hinge line at right angles. (The condition in *P. sugillata* is not stated but presumed to be as described herein.)

(iv) The anterior margin projects further in advance of the byssal groove in *P. sugillata* than in *P. carchariarum.*

(v) The dark band distal to the nacre on the non-nacreous margin characteristic of *P. sugillata* is absent in *P. carchariarum.*

(vi) The nacre of *P. carchariarum* has a distinct yellowish green tint, that of *P. sugillata* has not.

(vii) *P. carchariarum* is pale grey or greenish yellow externally with traces of four or five brown or green radial bands. *P. sugillata* is dirty greyish yellow with four or five brownish radial bands.

The author has examined a series of 17 separate valves of *P. a. carchariarum*, taken in commercial operations at Shark Bay, and several complete specimens in the Australian Museum collection. This material differs from *P. a. sugillata* in the following ways:

(i) The dark band distal to the nacre on the non-nacreous margin is completely absent in all specimens.

(ii) In some older specimens the nacre is perfused with a golden tint richer than the brassy yellow tint sometimes seen in *P. sugillata*.

(iii) There are only very faint traces of coloured rays on the external surface of the shell.

Examination of the other characters given by Jameson, in the light of the previous discussion of taxonomic characters, will show them to be almost valueless. Thus the identity of the material is determined by the colour of the nacre, the non-nacreous border, and the external surface of the shell. In the author's opinion such differences are at most of subspecific rank and accordingly Jameson's species should be reduced to a subspecies of *P. albina*.

Examination of other collections from the north-western Australian coast reveals that the differences between *P. a. sugillata* and *P. a. carchariarum* may not be as clear-cut as they appear above. In a collection of 120 specimens from Exmouth Gulf, 100 miles north of Shark Bay, one specimen possessed a prominent dark band distal to the nacre and two specimens were dark brown externally while a few more showed fairly prominent external rays. The remainder appeared to be typical *carchariarum* except that a yellowish green rather than a yellow colour showed in the nacre of some of the older specimens. In a collection of 157 specimens from Roebuck Bay, 54 specimens possessed a more or less prominent dark band distal to the nacre while seven specimens were either dark-coloured or showed a prominent rayed pattern. Many of these also showed a yellowish green rather than a yellow colour in the nacre. It is possible therefore that a cline exists in the characters separating the two subspecies.

(*d*) *Distribution*

Jameson (loc. cit.) recorded *P. carchariarum* from Shark Bay, Derby, and Kimberley but it seems best at the present time to restrict the distribution to the type locality.

The subspecies occurs most commonly in Shark Bay on "grassy" banks in 0-2 fm of water. There is no record of the species from deeper water.

VII. DOUBTFUL SPECIES AND RECORDS

Avicula flexuosa Reeve (1857, pl. 4, sp. 4).—Reeve's name is preoccupied by *A. flexuosa* d'Orbigny (1850). Reeve figures a rather distorted specimen which probably belongs to *P. margaritifera, P. fucata,* or *P. a. sugillata.* Reference to the type specimen is necessary to allocate Reeve's species to the synonymy of one of the three above.

Avicula placunoides Reeve (1857, pl. 17, sp. 68).—Reeve's species is a synonym of either *P. fucata* or *P. a. sugillata* but it is impossible to discriminate further on Reeve's description and figure.

Meleagrina margaritifera Cooke (1886, p. 136).—Cooke notes this species as occurring in South Australia. It is impossible to assign this reference to a synonymy.

Meleagrina muricata Cooke (1886, p. 136).—Cooke records this species from northern and South Australia. From the list of synonyms given by Cooke (loc. cit., p. 137) it is evident that he is confusing *P. fucata* and *P. a. sugillata* and his record belongs in the synonymy of either or both of these species.

Pinctada carchariarum Cotton and Godfrey (1938, p. 81).—This species was recorded as occurring in the subfossil state in South Australia, being common at Murat Bay. Subsequently Cotton (1949, p. 15) figured a fossil "pearl oyster" from South Australia. It is not clear whether he regards the two as synonymous. From the shape of the shell and the outline of the muscle scar the "pearl oyster" figured by Cotton (1949) is a *Pteria.* It is possible that the material seen by Cotton and Godfrey (1938) may belong in the same genus.

The following references do not refer to species in the genus *Pinctada*:

Meleagrina meleagridis Paetel (1890, p. 205),
M. ovata Paetel (1890, p. 205),
Pinctada papilionacea Hedley (1916, p. 155),
P. zebra Hedley (1916, p. 156),
P. physoides Hedley (1916, p. 156),
P. virens Hedley (1916, p. 156).

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LIST OF SPECIES

Genus *Pinctada*

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P. albina carchariarum (Jameson) 132
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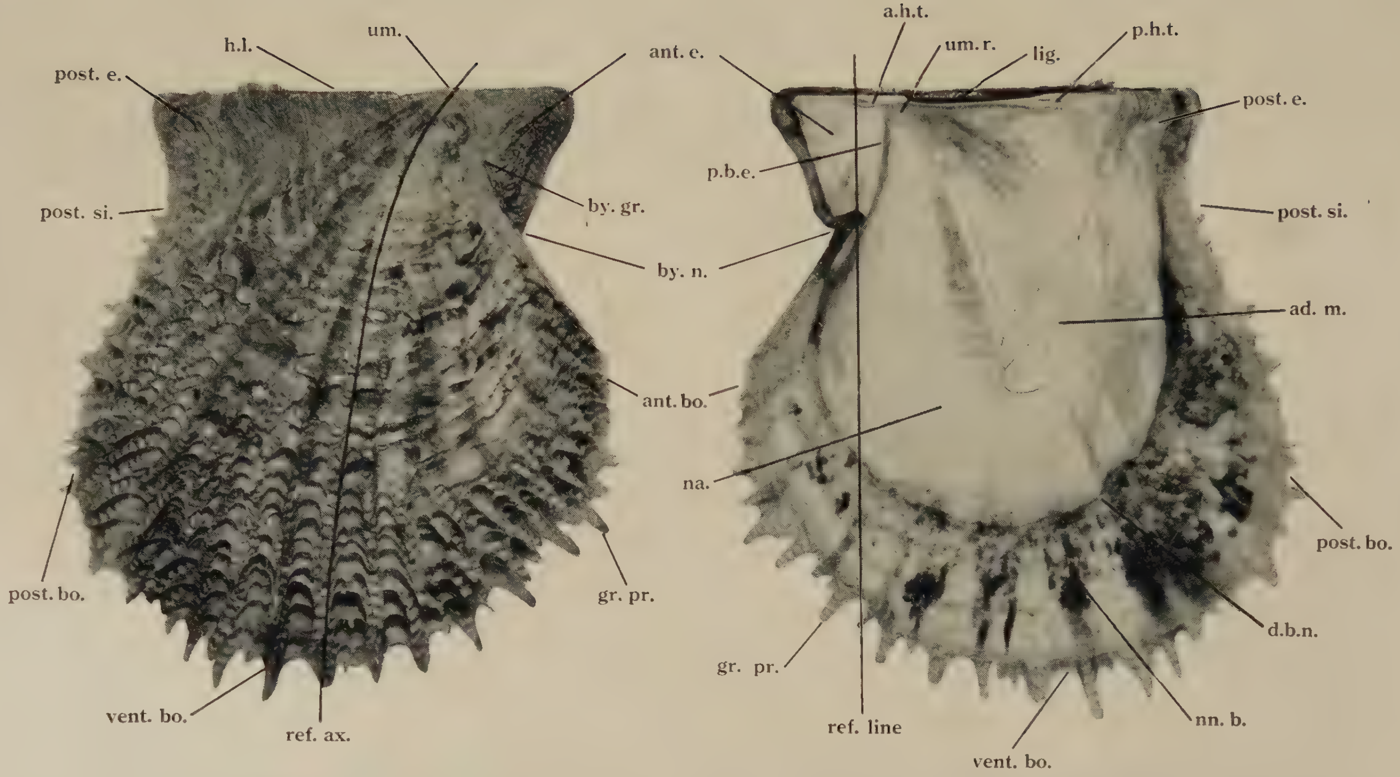
P. maxima (Jameson) 110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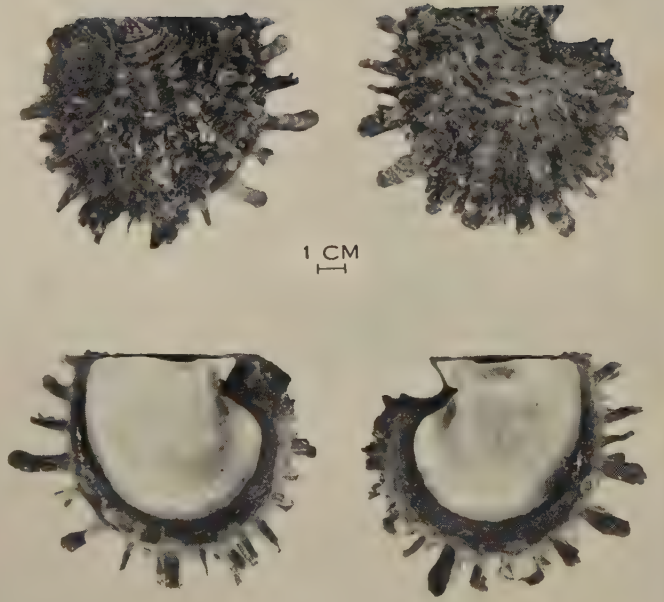
Right valve of a specimen of *P. fucata* (Gould) from hull of A. K. *Penguin*, Torres Strait, 14.xii.1950, showing shell structures and regions referred to in the text. *Ad. m.*, adductor muscle scar; *a.h.t.*, anterior hinge tooth; *ant. bo.*, anterior border; *ant. e.*, anterior ear; *by. gr.*, byssal groove; *by. n.*, byssal notch; *d.b.n.*, distal border of nacre; *gr. pr.*, growth process; *h.l.*, hinge line; *lig.*, ligament; *na.*, nacre; *nn. b.*, non-nacreous border; *p.b.e.*, posterior border of ear; *p.h.t.*, posterior hinge tooth; *post. bo.*, posterior border; *post. e.*, posterior ear; *post. si.*, posterior sinus; *um.*, umbo; *um. r.*, umbonal recess; *vent. bo.*, ventral border; *ref. ax.*, reference axis; *ref. line*, reference line.



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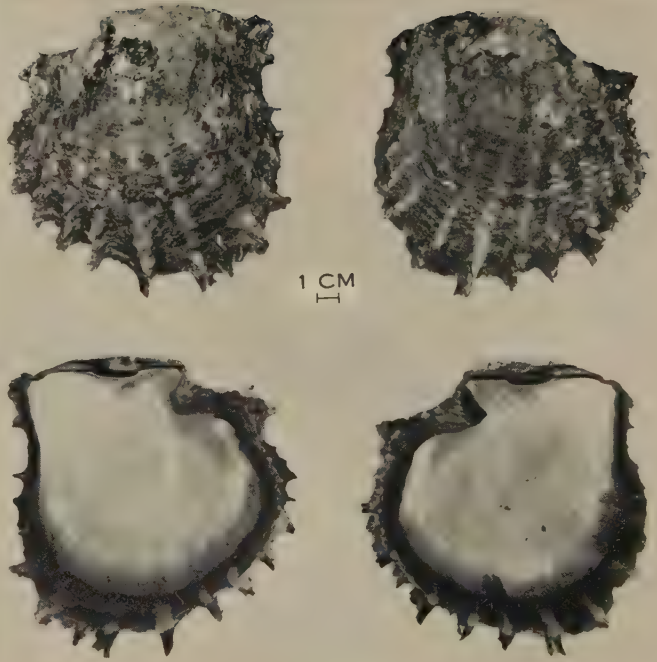

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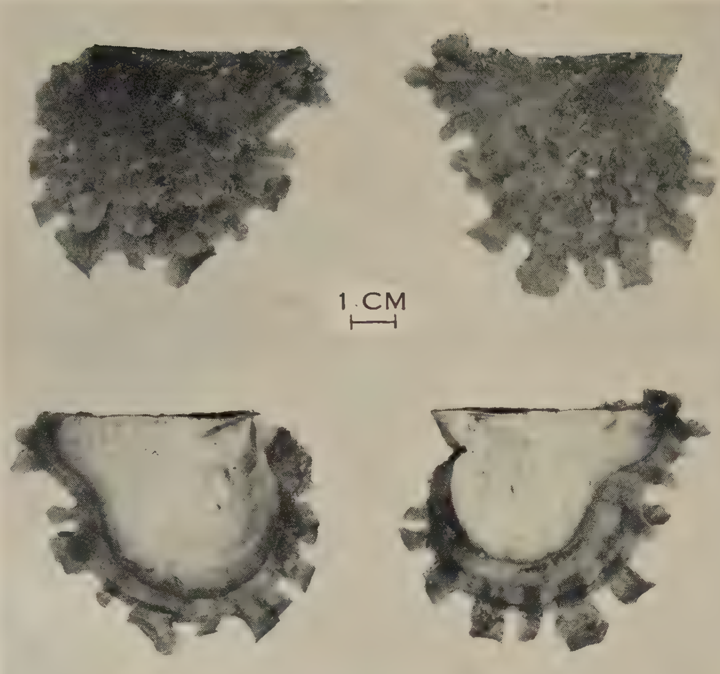
Fig. 1.—Young specimen of *P. margaritifera* (Linnaeus) from hull of M.V. *Pelai*, Thursday I. harbour, 20.xii.1952, age approx. 15 months.

Fig. 2.—Full-grown specimen of *P. margaritifera* (Linnaeus) from lower intertidal zone, Blackwood Bay, Mt. Adolphus I., Torres Strait, 16.v.1953.



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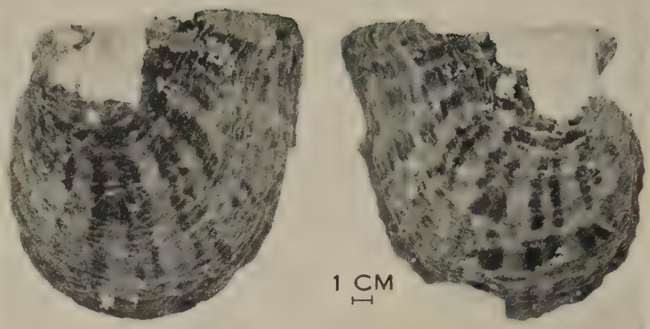

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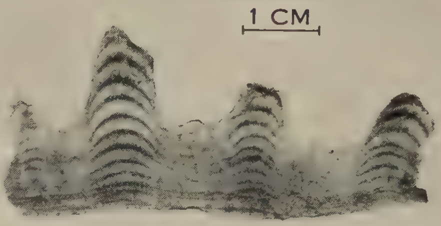

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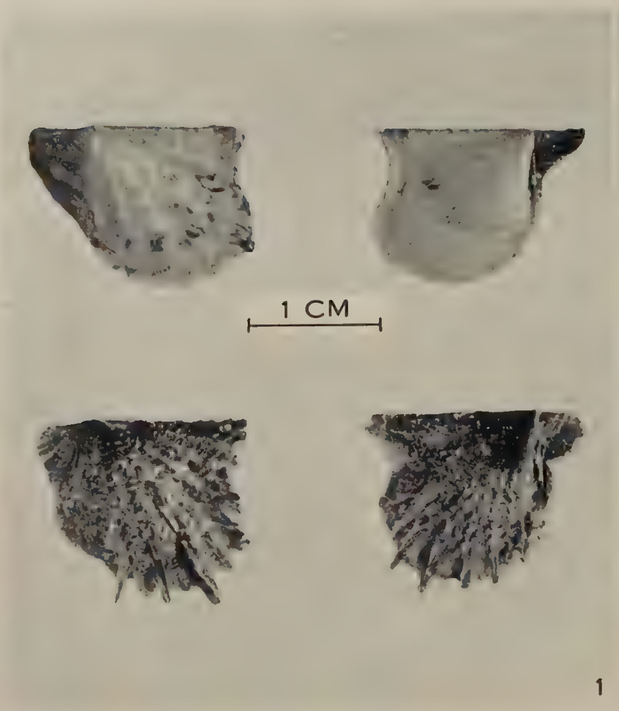
Fig. 1.—Young specimen of *P. maxima* (Jameson) taken off West I., Torres Strait, in 8 fm, 22.vi.1953.

Fig. 2.—*P. maxima* (Jameson) taken off Ranjeeri Point, Arnhem Land, Gulf of Carpentaria (opposite Groote Eylandt), in 10 fm, 5.ix.1952. The specimen is green with prominent dark green rays.

Fig. 3.—Portion of the lip of *P. maxima* (Jameson) taken on "Old Grounds", west of Badu I., Torres Strait, in 7 fm, 20.x.1949, showing growth processes with transverse banding.

REVISION OF THE AUSTRALIAN PEARL-SHELLS



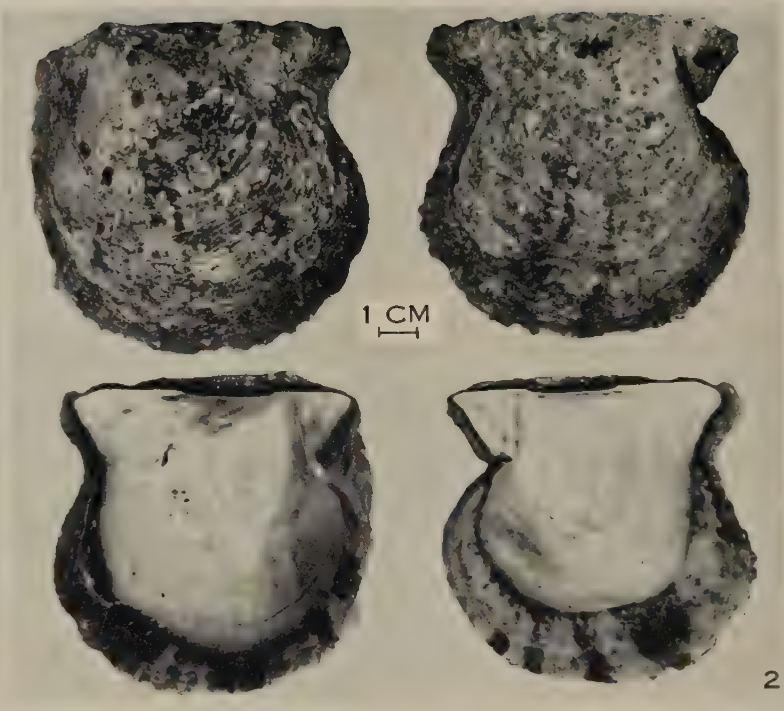


Fig. 1.—Two very young specimens of *P. fucata* (Gould) approximately 6 weeks after setting. From spat plates, Thursday I. harbour, Torres Strait.

Fig. 2.—Full-grown specimen of *P. fucata* (Gould) from intertidal bank, Iwaitcha Bay, Groote Eylandt, 22.viii.1952.

REVISION OF THE AUSTRALIAN PEARL-SHELLS

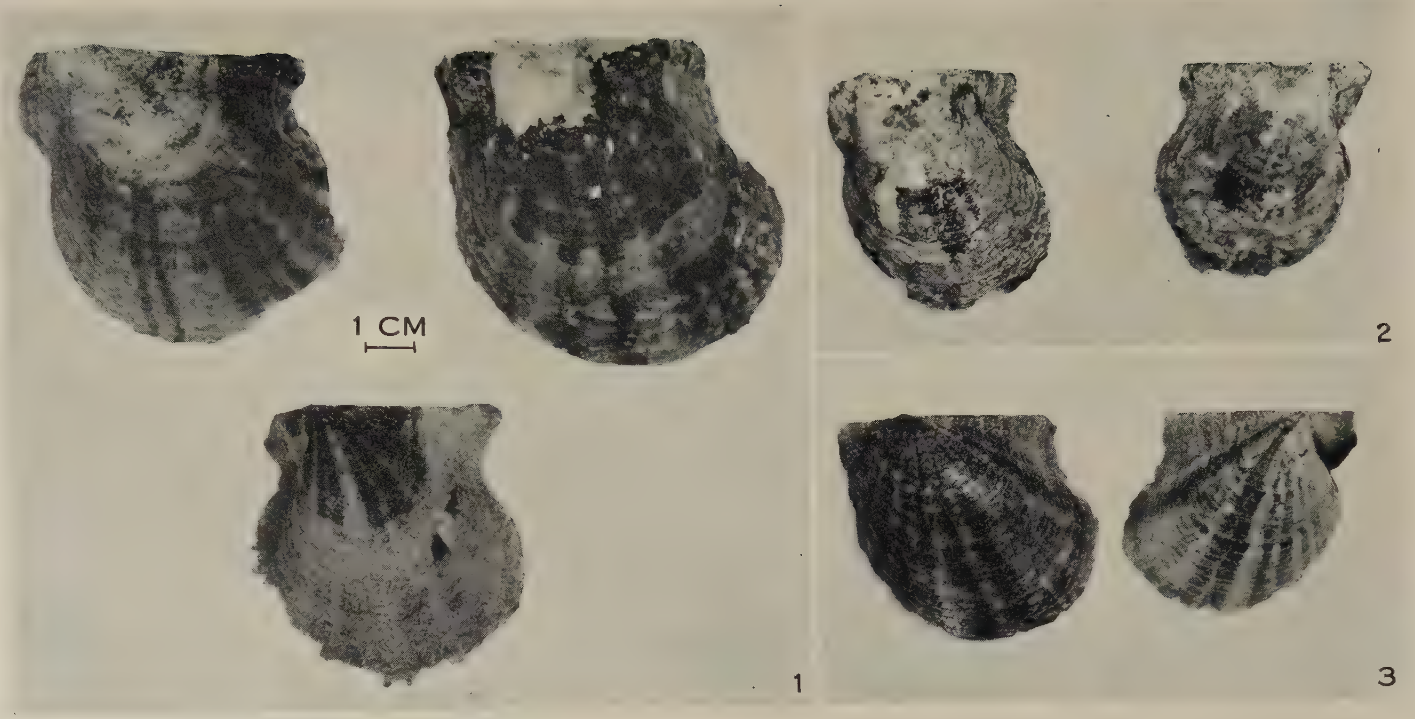


Fig. 1.—Three left valves of *P. fucata* (Gould) from culture cages, Thursday I. harbour, showing changes in external markings.

Fig. 2.—*Avicula fucata* Gould. Holotype U.S.N.M. Cat. No. 5935.

Fig. 3.—*Avicula lurida* Gould. Holotype, U.S.N.M. Cat. No. 5936.

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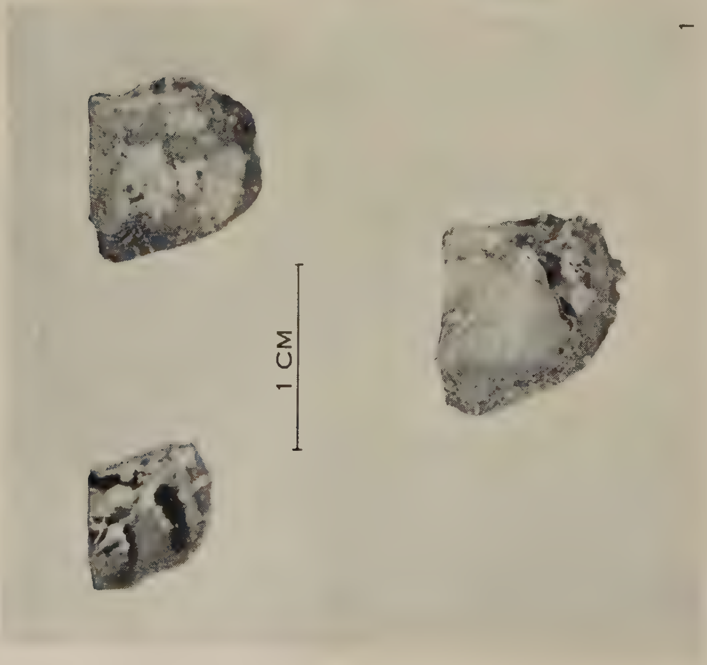

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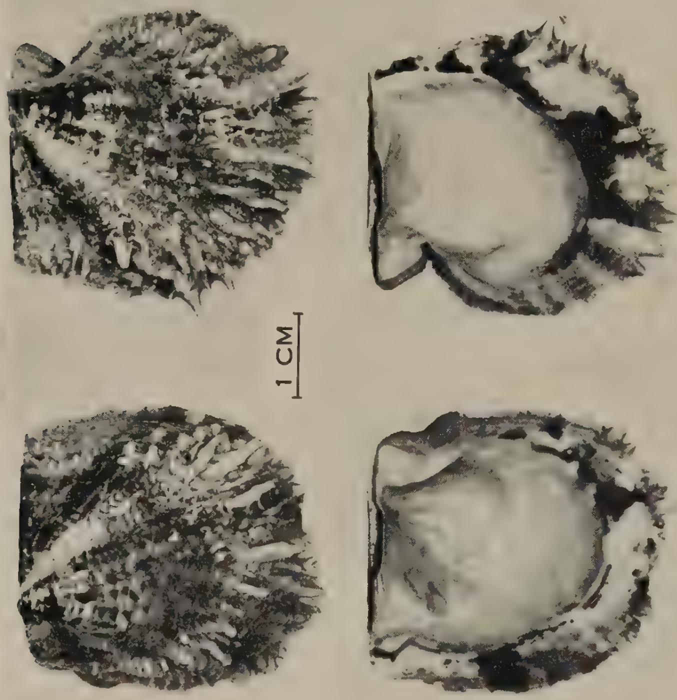
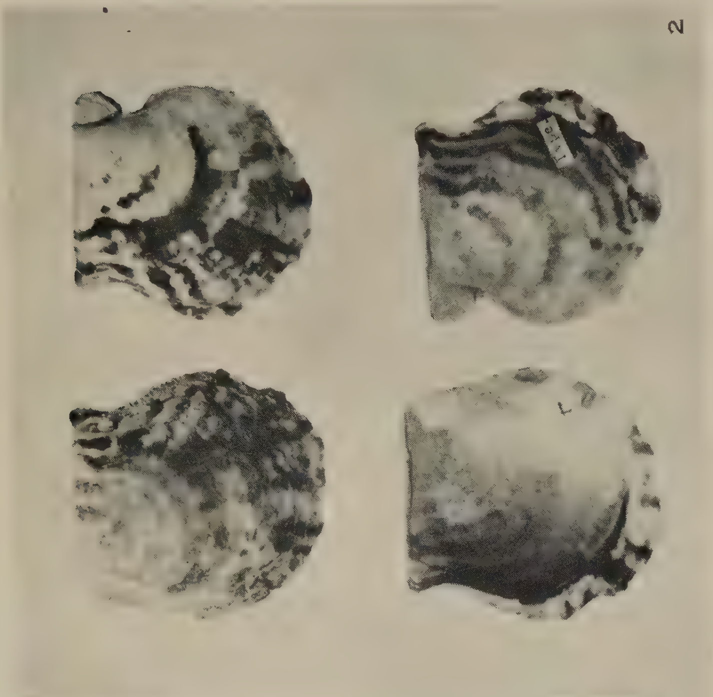


Fig. 1.—Three very young specimens of *P. maculata* (Gould) from Reef I., Santa Cruz Group. Taken among coral in lagoon. Aust. Mus. Cat. No. C52138.

Fig. 2.—A half-grown specimen of *P. maculata* (Gould) from Mangareva, Paumotu Is. Aust. Mus. Cat. No. C17196.



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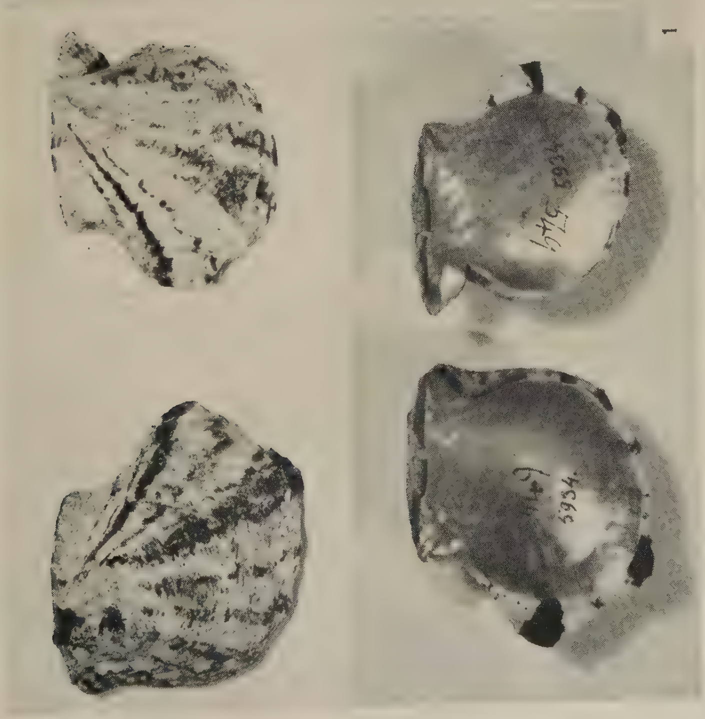

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Fig. 1.—*Avicula maculata* Gould. Holotype, U.S.N.M. Cat. No. 5934.
Fig. 2.—*Margaritifera panasesae* Jameson. Holotype, B. M. (N.H.) Cat. No. 1901-3-25.2.

REVISION OF THE AUSTRALIAN PEARL-SHELLS

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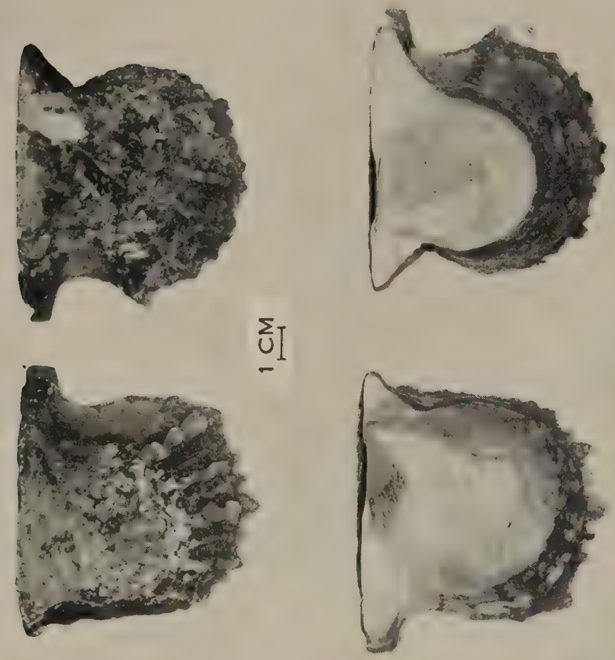

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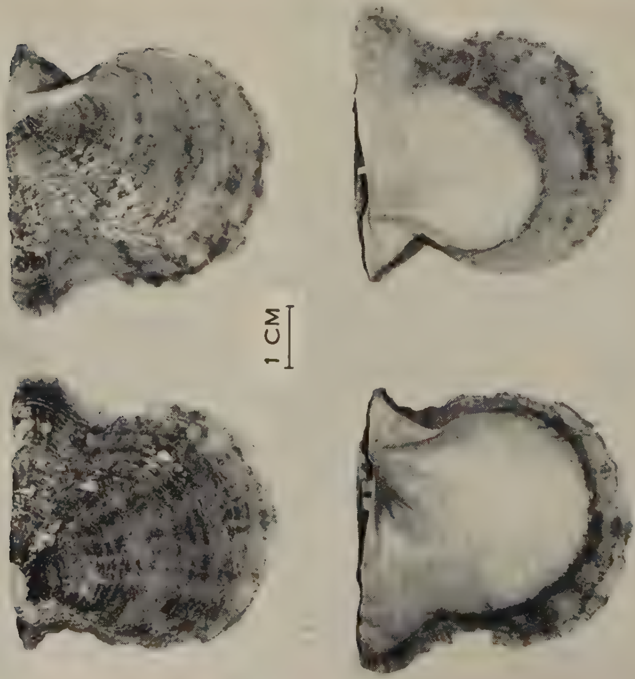

Fig. 1.—Young specimen of *P. chemnitzi* (Philippi) from Keppel Bay. Aust. Mus. Cat. No. C58514.

Fig. 2.—Full-grown specimen of *P. chemnitzi* (Philippi) from intertidal reef near Crab I., Cape York Peninsula.

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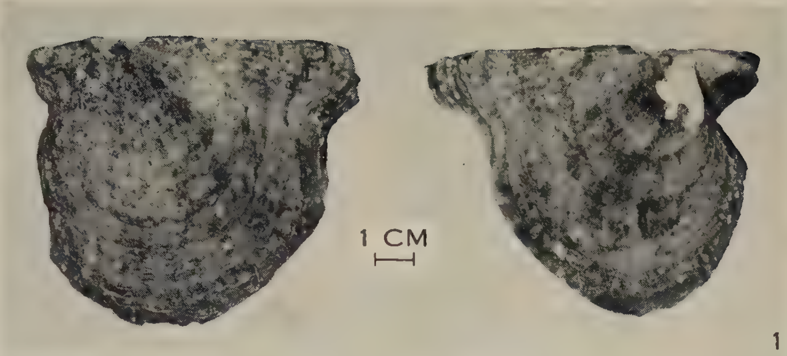

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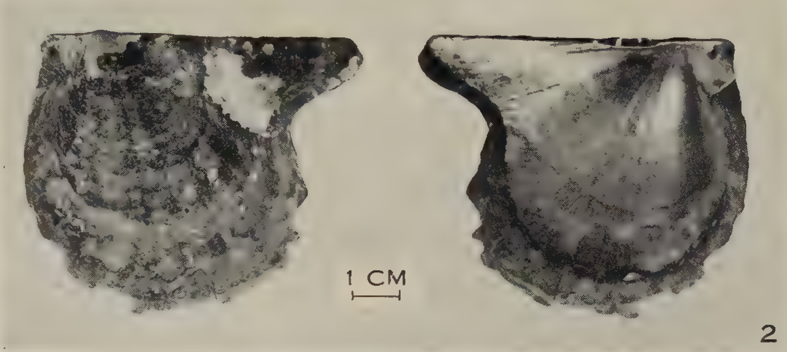

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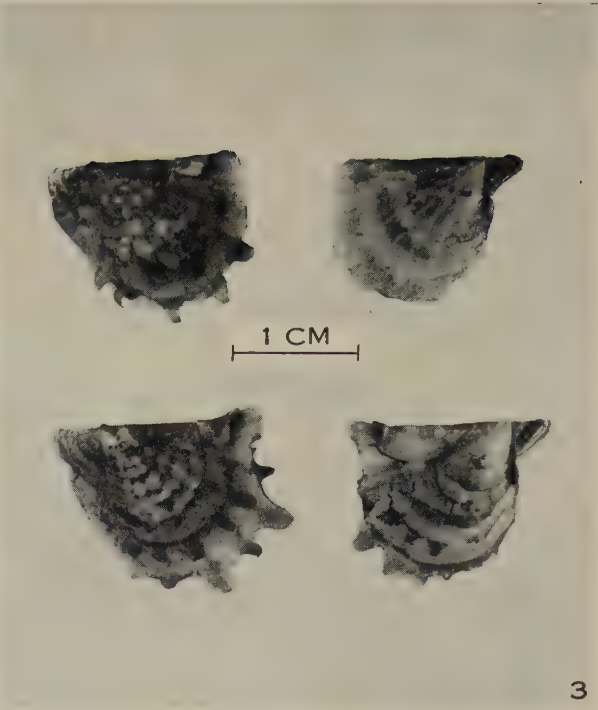

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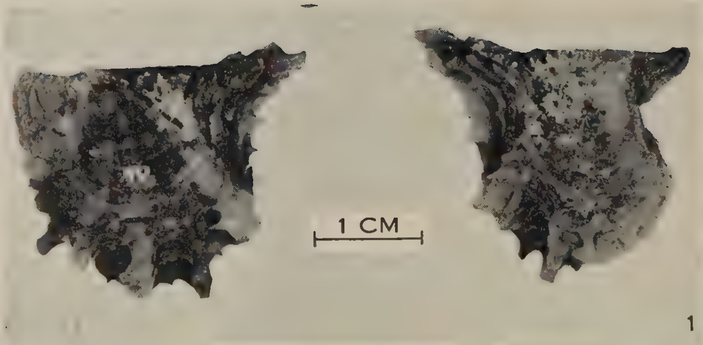
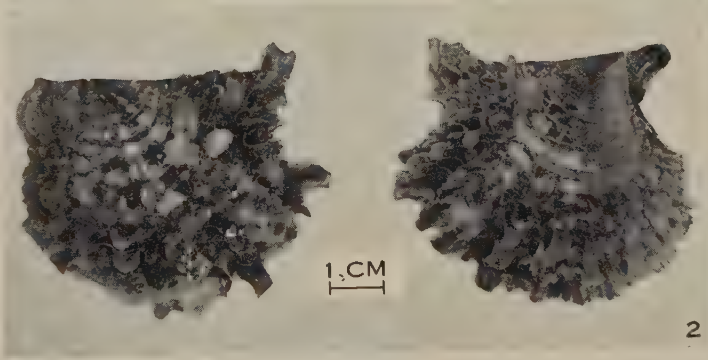
Fig. 1.—Full-grown specimen of *P. chemnitzi* (Philippi) from Yirrkala, near Cape Arnhem, Gulf of Carpentaria. Aust. Mus. Cat. No. C61344.

Fig. 2.—*Pinctada epitheca* Iredale. Holotype, Aust. Mus. Cat. No. C60343.

Fig. 3.—Two very young specimens of *P. albina sugillata* (Reeve) approximately 6 weeks after setting. From spat plates, Possession I., Torres Strait.

REVISION OF THE AUSTRALIAN PEARL-SHELLS





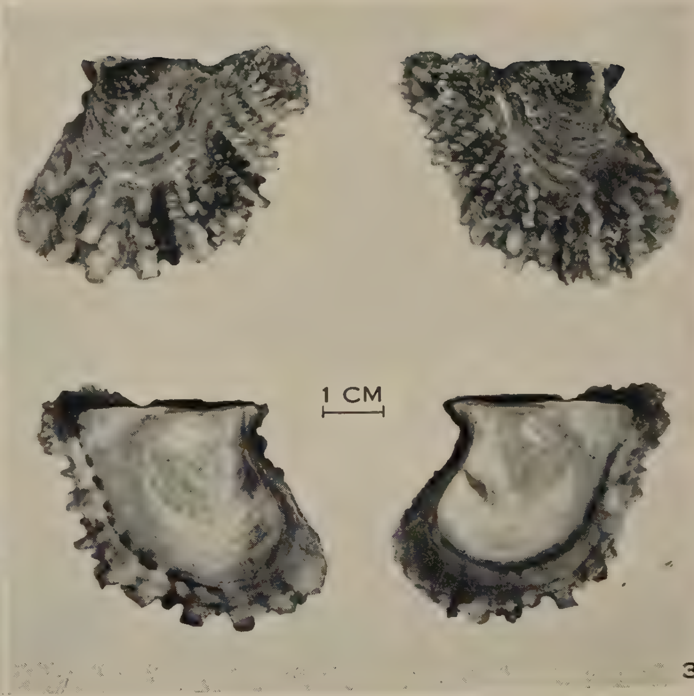
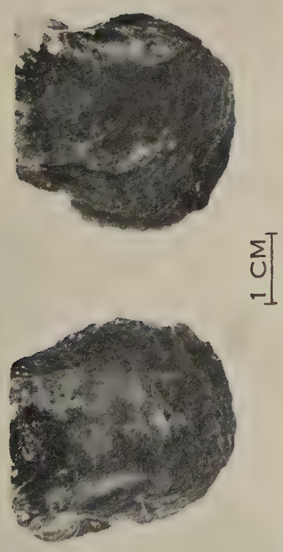


Fig. 1.—Young specimen of *P. albina sugillata* (Reeve) from intertidal bank, Scharapa Passage, Groote Eylandt, 28.vii.1952.

Fig. 2.—Half-grown specimen of same species from hull of A. K. *Penguin*, Thursday I. harbour, 14.xii.1950.

Fig. 3.—*P. albina sugillata*, obtuse specimen from flat coral rock in lower intertidal zone, Friday I., Torres Strait, 28.vii.1952.

REVISION OF THE AUSTRALIAN PEARL-SHELLS



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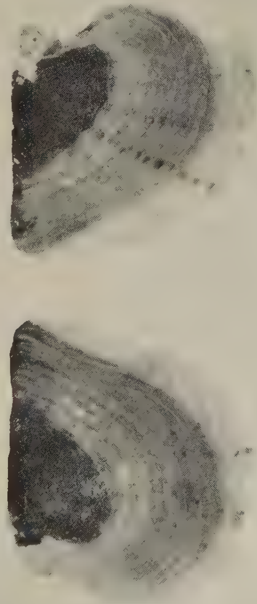

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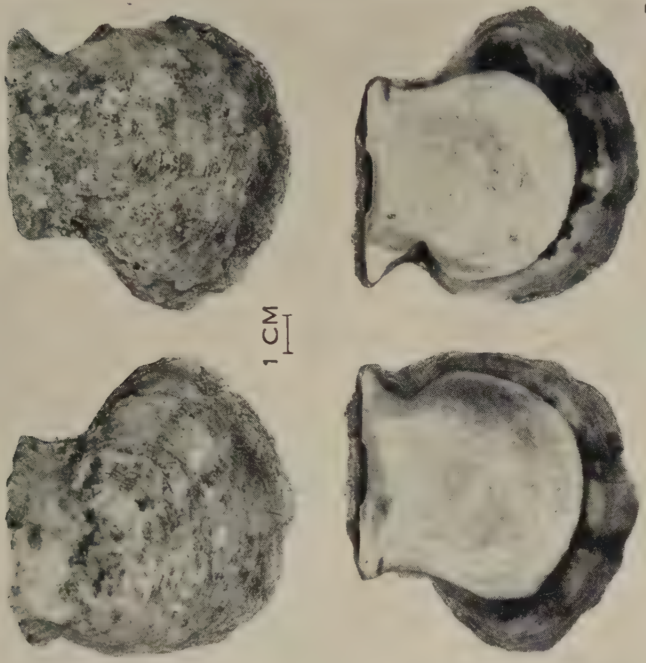

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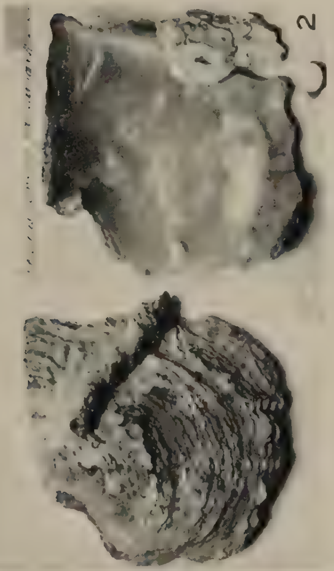
Fig. 1.—*Pinctada perrutila* Iredale. Paratype, Aust. Mus. Cat. No. C18787.

Fig. 2.—*P. albina sugillata* (Reeve) from Kurnell, Botany Bay. Aust. Mus. Cat. No. C61646.

Fig. 3.—Full-grown specimen of *P. albina sugillata* (Reeve) from intertidal bank, Scharapa Passage, Groote Eylandt, 26.vii.1952.

REVISION OF THE AUSTRALIAN PEARL-SHELLS



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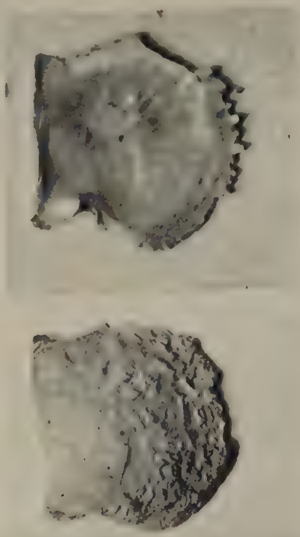

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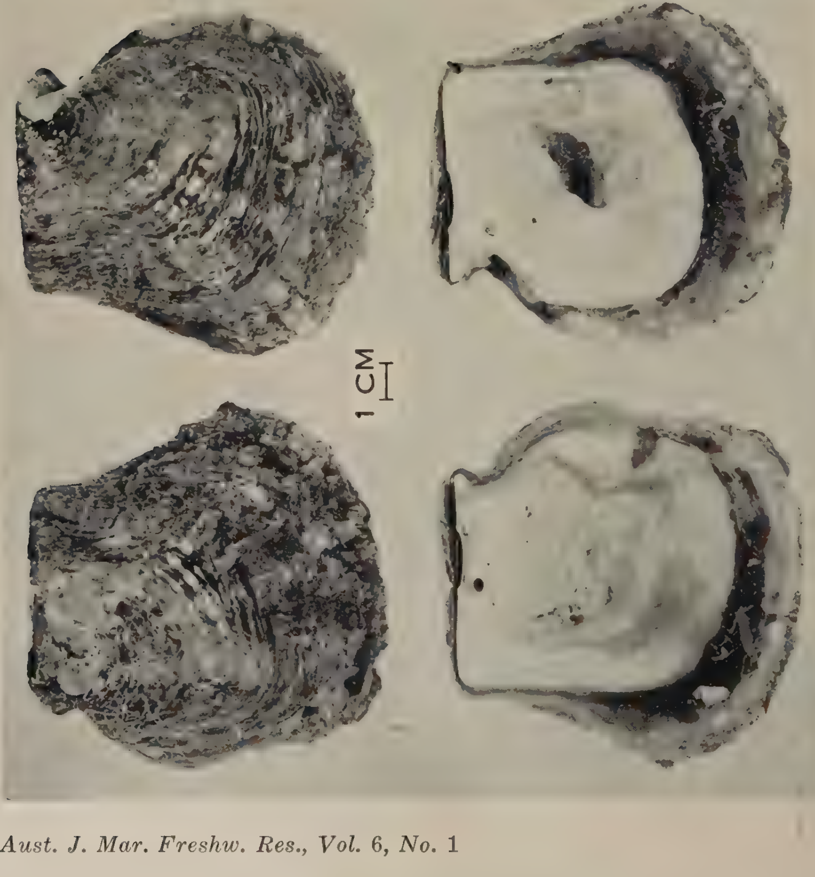

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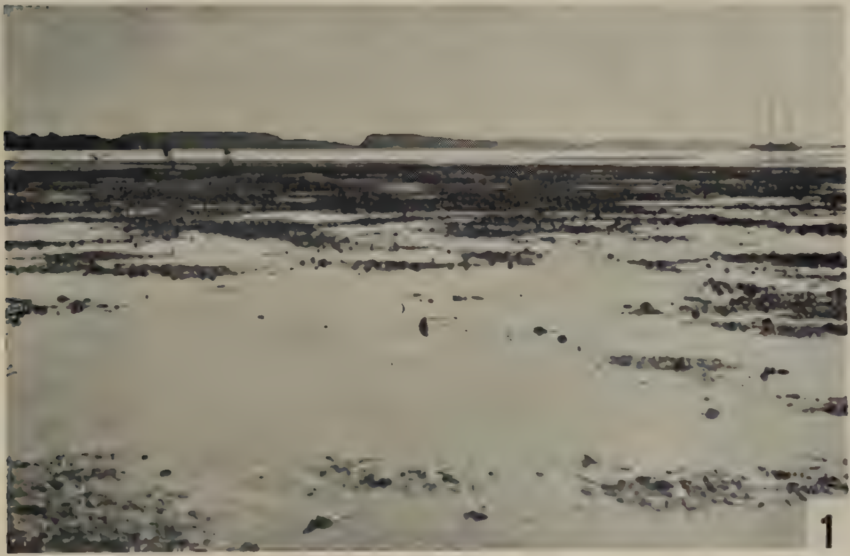
Fig. 1.—Full-grown specimen of *P. albina sugillata* (Reeve) from lower intertidal zone, Barney I., Torres Strait, 25.vi.1953.

Fig. 2.—*Meleagrina albina* Lamarck. Holotype, Mus. d'Hist. Nat. Paris.

Fig. 3.—*M. albina* Lamarck. Paratype, Mus. d'Hist. Nat. Paris.

REVISION OF THE AUSTRALIAN PEARL-SHELLS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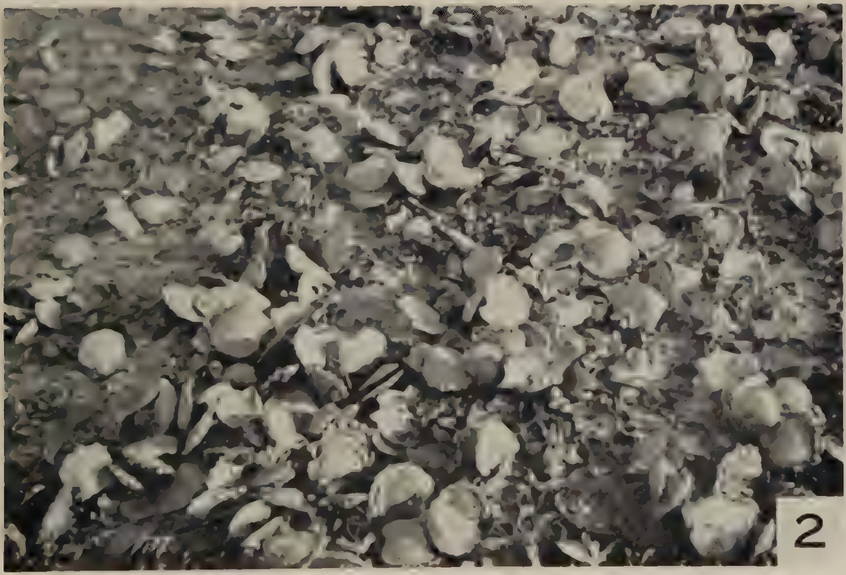
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Fig. 1.—View of intertidal bank, Scharapa Pasage, Groote Eylandt, at low tide. The F.R.V. *Gahleru* is in the right background. Photo, J. L. H. Wassell.

Fig. 2.—Close-up of portion of the same bank, showing a profusion of *P. albina sugillata* (Reeve). Photo, J. L. H. Wassell.

STUDIES OF THE BLOOD AND TESTS OF SOME AUSTRALIAN ASCIDIANS

II. THE TEST OF PYURA STOLONIFERA (HELLER)

By R. ENDEAN*

(*Manuscript received October* 27, 1954)

Summary

The test of this species is particularly bulky and consists of gelatinous material which encloses the fleshy part of the animal, leaving openings only for the two siphons. It also forms a resilient basal stem which anchors the animal to the substratum. The outer surface of the test is impregnated with sand grains, which form a hard protective layer.

Blood-vessels traverse the gelatinous material. Two large vessels enter the test and these branch to form ultimately a ramifying system of small blood-vessels. Effectively there are two blood circulations in the test. The blood-vessels have a lining consisting of a single layer of large columnar cells, the appearance of which is described.

The gelatinous test resolves itself under the microscope into a network of fibres of variable thickness, but the larger ones at least are aggregates of smaller fibrils. In some cases the fibres are orientated in definite directions. The amorphous interfibrillar material seems to be mainly aqueous, as the test consists of over 97 per cent. of plasma.

Ferrocytes wander about in amoeboid fashion amongst the fibres. These enter the substance of the test by migrating across the walls of the blood-vessels. Histologically there is a marked similarity between the appearance of the test and that of vertebrate connective tissue, as in both cases cells are present in a groundmass enmeshed by fibres which stain with orcein and fuchsin.

However, the fibres of the test are composed of a very insoluble polysaccharide, which although resembling plant cellulose in certain respects will not dissolve in special cellulose solvents nor stain with cellulose stains. A mucopolysaccharide which stains metachromatically with toluidine blue is associated with the fibrillar material, and possibly serves to cement the fibres together since these became disarranged on treatment with hyaluronidase, which removes the mucopolysaccharide.

The importance of the test in the general economy of the animal is discussed.

I. INTRODUCTION

The ascidian test is unique in containing tunicin, a substance closely resembling cellulose in its physico-chemical properties. Consequently it has been the subject of numerous investigations over the last century. The earlier work is well summarized by Saint-Hilaire (1931).

The test of all species examined contains fibres, embedded in a structureless groundmass, and the so-called "test cells", which in the

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Didemnidae and Clavelinidae at least are merely blood cells—some types of which are in various stages of degeneration (Pérès 1945, 1948*a*). In the monascidians and in the Botryllidae blood-vessels with a lining consisting of a single layer of epidermal cells course through the test.

Analyses of the test have shown that it contains a large percentage of water. Saint-Hilaire (1931) found that the "cartilaginous" test of *Ascidia mentula* Müller contains 90 per cent. of water whilst the "membranous" test of *Pyura papillosa* (Linnaeus) contains 65 per cent. of water. In *Ciona,* inorganic salts, nitrogenous material, and cellulose comprise the residual material (Payen, quoted by Brien 1948). Saint-Hilaire (1931) has shown that the fibres are richer in nitrogenous material than the groundmass. Pérès (1948*b*), on the basis that the ascidian tunic exhibits metachromatic staining with toluidine blue, states that it consists of cellulose accompanied by proteins "qui sont sans doubte des glycoprotéides dont le groupement prosthetique est un ester sulfurique de polysaccharide de poids moléculaire élevé".

This paper describes the structure of the test of *Pyura stolonifera,* reports on the results of histochemical and chemical investigations made on the test, and shows as far as possible the arrangement and function of the chemical constituents within the test.

II. Materials and Methods

The ascidians used in this investigation belong to the two environmental forms of *P. stolonifera.* The rocky ocean shore form was obtained from Maroubra Bay, N.S.W., and subsequently from Currumbin, Qld. The estuarine form was obtained from Port Hacking, N.S.W. Part I of this series (Endean 1955) contains descriptions and drawings of these forms.

Methods used in particular investigations are described under relevant headings.

III. Gross Structure of the Test

The test of both forms consists essentially of an inner core of gelatinous material bounded by a thin external layer of inorganic material consisting chiefly of sand grains. The test completely encloses the sac-like fleshy portion of the animal, leaving spaces only for the passage of inhalant and exhalant siphons.

Figure 1 shows the general dimensions of the test and its relationship to the remainder of the animal in a typical adult specimen of the rocky ocean shore form. The test volume in the specimen drawn would approximate to 350 c.c. At the region of attachment to the substratum, strands of gelatinous test force their way into crevices in the rock. If this rock is of the soft sedimentary type, pieces of it are frequently found embedded in the base of the test when the animal is removed from its natural habitat. Sometimes the animal is so firmly attached to the underlying rock that it is necessary to chip away pieces of the rock before it can be dislodged. The importance of such a mode of attachment in the economy of an animal that inhabits a zone on the sea-shore particularly susceptible to the battering of the surf is obvious. The long basal stem of the test is sufficiently resilient to enable the animal to bend slightly in the surge of the waves without rupture of the test. Embedded sand grains forming a layer 1-3 mm thick impart to the external region of the test a tough leathery consistency which protects the animal from the effects of abrasive particles suspended in the water. Usually an assemblage of fouling organisms (algae, barnacles, etc.) is found adhering to this external layer.

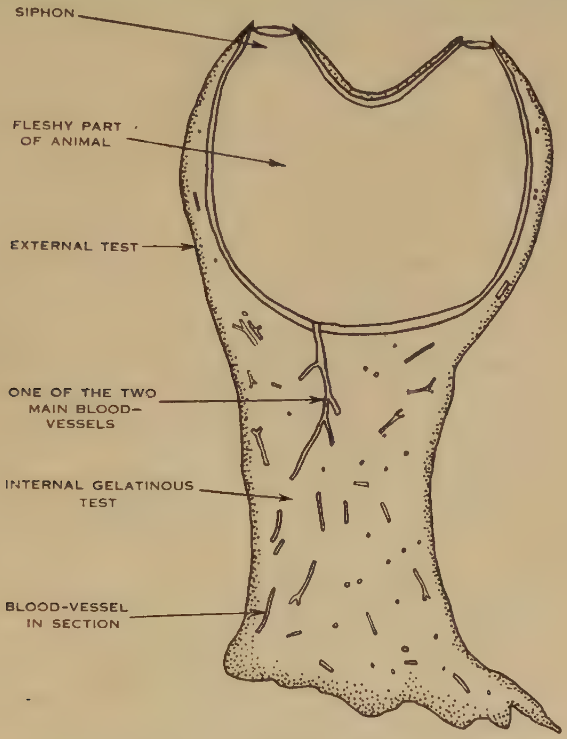


Fig. 1.—Sagittal section through rocky ocean shore form of *P. stolonifera.* × ½. Semi-diagrammatic.

Figure 2 shows the dimensions of the test in a typical adult specimen of the estuarine form. The test of this form is even bulkier than in the rocky ocean shore specimens. The long root-like processes arising from the test serve to anchor the animal in the sand of the estuary. The external layer is more brittle and coriaceous than in the oceanic form. Fragmented mollusc shells are frequently found adhering to the long "roots".

In both forms there is occasional evidence of attempts by organisms to bore into the test. The damaged portion of the gelatinous test is brown and if there is a cavity this is filled with a brownish fluid. In no case was a living organism of macroscopic dimensions found in the test. However, the rocky ocean shore form had frequently overgrown the calcareous tubes of the serpulid *Galeolaria caespitosa* Lam. and also several species of barnacles.

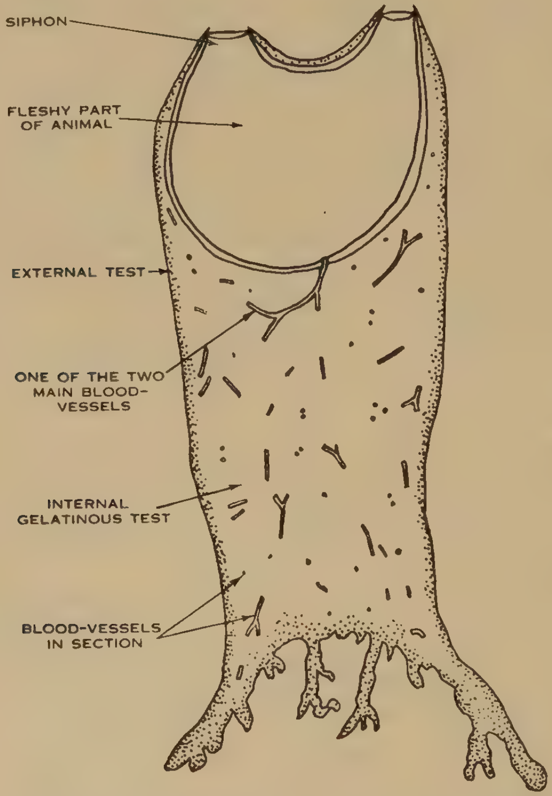


Fig. 2.—Sagittal section through estuarine form of *P. stolonifera.* × ½. Semi-diagrammatic.

In both forms the test contains blood-vessels. Those of the rocky shore variety have purplish walls and their course through the transparent test is readily determined. Two main trunks enter the test from the base of the fleshy part of the animal and arise from the subendostylar and the perivisceral sinuses respectively. These two trunks, which are about 0.8 mm in diameter, run the length of the test but, although they may cross one another in close proximity, they have not been observed to intersect in any of the specimens examined. Vessels with diameters ranging from 0.3 to 0.7 mm arise from these main trunks in all planes and pursue varied courses through the test. Some turn through nearly 180° and pass into the thin test surrounding the fleshy part of the animal. Others branch and proceed to points in the test sometimes diametrically opposite one another. Sometimes the vessels bend and run for several centimetres parallel to and just below the hard external test. None of these major vessels arising from one trunk has been observed to join with those having their origin in the other trunk.

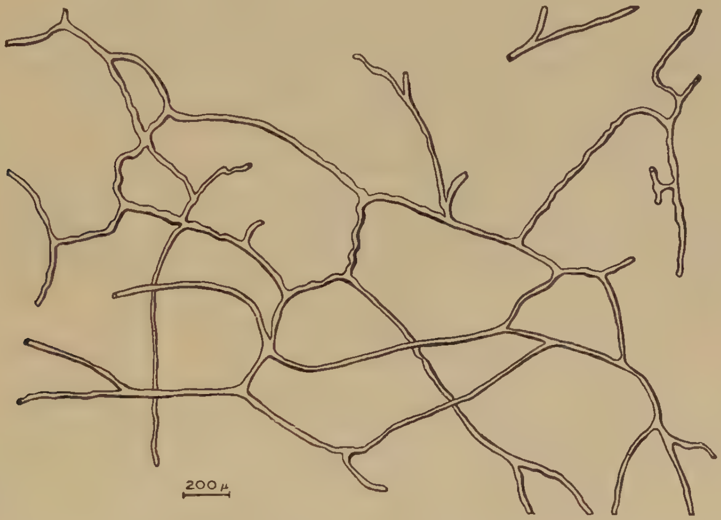


Fig. 3.—Small blood-vessels in a thin section of test, showing manner in which these vessels branch.

The main trunks and the large vessels just discussed give rise to innumerable small vessels averaging about 35 μ in external diameter which ramify through the gelatinous material, anastomosing extensively (Fig. 3). In the core of the test most of these small blood-vessels seem to be oriented principally in a direction parallel to the long axis of the animal. However, towards the outer region of the test they form a fairly regular network. The smaller vessels near the fleshy part of the animal are frequently convoluted, whilst those in the test nearer the point of attachment follow fairly straight paths before intersection. This could be interpreted as being due to stresses imposed on the test by the environment—the region of the test where the convoluted vessels are found being thinner and hence more flexible.

In some specimens but not in others, there is an aggregation of the fine blood-vessels in the cores of the tests, particularly just below the base of the fleshy parts of the animals. This gives the appearance of vascular strands running for varying distances down the long axes of the animals. The origin of these aggregations is obscure.

Some of the outer blood-vessels of the test enter the hard external layer, where they appear to end blindly against sand grains.

There are effectively two blood circulations in the test. When the heart beats in one direction blood fills one system of major vessels and is drained from the other and when the heart beats in the other direction the blood flow is reversed. It has not been ascertained as yet whether there is connexion in the test between the two major systems of vessels by way of the small anastomosing vessels just discussed. However, these vessels ramify and branch so extensively and their internal diameters are so small that it is doubtful whether a significant interchange of blood between the major systems of vessels in the test would occur.

The blood-vessels of the estuarine form are colourless. However, when living specimens were placed overnight in sea-water containing neutral red (1: 10,000), the blood-vessels in the test became bright red owing to the staining *in vivo* of contained blood cells. The course of the blood-vessels in the tests of both forms was fundamentally similar except for the fact that the blood-vessels extend into the long root-like processes of the estuarine variety.

IV. Microscopic Structure of the Test

Pieces of the gelatinous test were fixed variously with Bouin's mixture, Susa, Carnoy's fluid, 5 per cent. formalin, and equal parts of 8 per cent. basic lead acetate and 16 per cent. formalin. Because of the dense nature of the material prolonged fixation and vacuum embedding were necessary. Care had to be taken in sectioning because of the frequent occurrence of sand grains.

Sections ($10\ \mu$) were stained initially with Mallory's triple stain and examined. The test was found to consist of fine fibres, which stained blue, blood-vessels, the walls of which stained reddish, and blood cells, which also stained reddish. Blood cells were present both in the blood-vessels and between the fibres. A variety of stains was then used. The fibres were found to have a strong affinity for Unna's orcein and this stain was much used in studying them. Chlorazol Black E, which stained the fibres purplish grey, and Light Green, which stained them green, were also useful. Mann's eosin-methyl blue presented a very clear picture of the distribution of fibres, blood-vessels, and blood cells within the test and was used extensively whenever a composite picture of the microscopic structure of the test was desired.

Usually straight but sometimes convoluted, the test fibres interlaced in all planes, forming a network. They were of indeterminate length but some ran for as much as $60\ \mu$ before intersecting with others. Their diameter varied, the thicker ones being about $0.5\ \mu$ in diameter but the majority approx. 0.3-$0.4\ \mu$. Some regions of the sections showed uniformly thick fibres but in other regions both types intermingled (Plate 1, Figs. 1 and 2).

Some of the thinner fibres were on the limit of resolution and could not be distinguished with certainty from the structureless interfibrillar material. This raises the question as to whether the fibres are actually present *in vivo* or are artefacts. No matter what fixative was used fibres could be discerned, and phase contrast examination of thin slices of fresh test showed that the thicker fibres at least were present *in vivo*.

In some regions of the sections the fibres were more closely packed than in others. However, there was no regularity about the arrangement. The fibres appeared to have been under tension originally, because some of the more superficial ones had been cut during sectioning and had sprung back upon themselves. Silver impregnation of the fibres following Wilder's (1935) technique revealed that the thicker fibres at least were probably aggregates of thinner ones and this was confirmed by phase contrast examination.

An attempt was made to ascertain whether the fibres were regularly oriented. Small pieces from various parts of the test of different individuals were sectioned in various planes. Although some sections exhibited areas where the bulk of the fibres were oriented predominantly in one direction, other regions of the same sections showed the bulk of the fibres oriented in other directions, sometimes in undulating sheets. In general there was a tendency for fibres near the centre of the test to run parallel to the long axis of the test, and fibres near the exterior to run parallel to the external surface. This was particularly so in those fibres which formed the lining to the cavity surrounding the fleshy part of the animal. These fibres were thick and their close packing conferred an opaque appearance on the lining of the cavity. In the vicinity of the blood-vessels the test fibres were aggregated together to form thick fibre bundles which ran parallel to the long axes of these vessels (Plate 1, Fig. 3). In cross section the vessels were surrounded by concentric rings of these aggregated fibres (Plate 1, Fig. 4). These observations suggest that the blood-vessels have pushed their way through the meshwork of fibres after these fibres have been laid down. The concentrations of large fibres around the blood-vessels rendered the test in the immediate vicinity of these vessels somewhat opaque. In other regions of the test the fibres for the most part formed a random meshwork.

The smaller blood-vessels, which were fairly uniform in size, averaged about 12 μ in internal diameter and were circular in cross section. The larger vessels were three-pronged or four-pronged in cross section (Fig. 4). The length of each prong was variable but averaged about 65 μ. The main trunks, which averaged 700 μ in diameter, had slightly folded walls but were roughly circular in cross section.

The blood-vessels of the test were all lined with an epithelium which consisted of a single layer of large columnar epidermal cells. These cells (Fig. 5), which in the fixed condition averaged about 12 μ in height by 7 μ wide, each possessed a large nucleus with a prominent nucleolus. The nucleus was found in the distal half of the cell, a large vacuole being present usually in the basal half of the cell. Small vacuoles could be discerned at the apex of the cell, whilst there was some granular material in the vicinity of the nucleus. This region of the cell coloured strongly with basic stains, the staining being less intense towards the apex. Chlorazol Black E stained the nucleus light brown, the cytoplasm in the immediate vicinity of the nucleus dark brown, the basement membrane blue, and the vacuolated cytoplasm at the apex of the cell blue also.

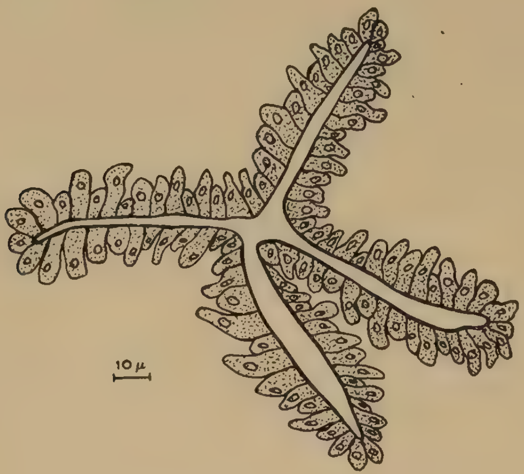


Fig. 4.—Transverse section of a "four-pronged" blood-vessel.

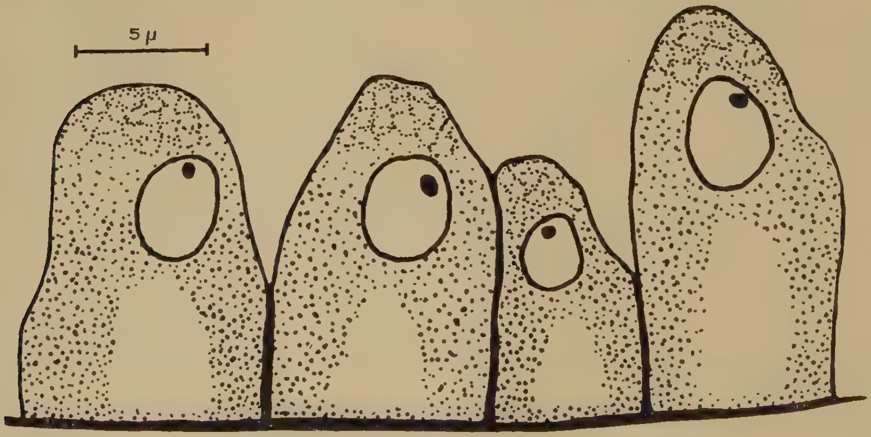


Fig. 5.—Four epidermal cells from the lining of a small blood-vessel. In each cell the prominent basement membrane, the large basal vacuole, the nucleus with nucleolus, granular cytoplasm, and the vacuolated apical cytoplasm can be seen.

Ferrocytes (see Endean 1955) were observed in all sections of the test. Use of the phase contrast microscope on fresh sections revealed that many of these corpuscles moved in amoeboid fashion amongst the fibres. Others were stationary and many of these appeared to be degenerating. Sometimes the cells were distributed fairly uniformly throughout the sections but frequently there were clusters of them in localized regions. Counts made with a squared eyepiece on 20 sections, each 10 μ thick and taken from various regions of the test, gave an average figure of 33,200 cells/mm^3 of test.

The question arises as to how the ferrocytes enter the test substance. As they are present in the blood-vessels, which ramify through the test, one mode of entry could be via the walls of these vessels. Such a passage could not be discerned with certainty in sections stained with azan or Mallory's triple stain, because the ferrocytes and the cells lining the blood-vessels stained similarly. Mann's eosin-methyl blue stained the blood cells red and the cells forming the walls of the blood-vessels orange. When the phase contrast microscope was used on sections stained with this stain the ferrocytes appeared blue and could be distinguished readily from the epidermal cells lining the blood-vessels. Some sections revealed the ferrocytes migrating through these cells.

It was thought that ferrocytes might also migrate across the epidermis of the fleshy part of the animal and enter the test substance by way of the cavity that separates this part of the animal from the test (see Fig. 1). However, examination of sections of the epidermis from the fleshy part of the animal failed to reveal any passage of ferrocytes. It was concluded, therefore, that ferrocytes enter the test substance only by migrating across the walls of the blood-vessels present in the test.

V. Histochemistry of the Test

(a) *Fibres*

The aniline blue component of the polychrome stains Mallory's and azan stained the test fibres blue. Weigert's fuchsin stained the fibres greyish and Unna's orcein stained them orange. Thus the staining behaviour of the fibres resembles that of the collagen fibres in vertebrate connective tissue.

It was considered likely therefore that the fibres might contain protein of the albuminoid type and attempts were made to detect protein histochemically. Frozen sections were stained for proteins containing tyrosine with Millon's reagent (Bensley and Gersh 1933) and for proteins containing arginine by following the method of Serra (1944). In both cases the fibres gave a very weak positive reaction. Formalin-fixed sections of the test were also subjected to the mercuric bromophenol blue technique of Mazia, Brewer, and Alfert (1953) for the cytochemical staining of protein. Negative results were obtained but after treatment with the reagent the fibres stood out sharply under phase contrast. Sections boiled with ninhydrin also gave negative results for protein. The results of histochemical staining for protein were therefore somewhat inconclusive but there appeared to be little if any protein present.

As it was felt that the presence of large quantities of polysaccharide, particularly polysaccharide linked to protein, might mask or interfere with the reaction of protein to histochemical reagents, polysaccharides were next sought histochemically. Sections of the test fixed in Bouin's mixture were employed and the method of Hotchkiss (1948) followed. The fibres of the test became reddish violet, indicating that they contained polysaccharide material.

Since all ascidians so far investigated have been found to contain tunicin or cellulose it was considered likely that the polysaccharide staining observed was due to cellulose. Attempts were made therefore to detect cellulose histochemically. Frozen sections were treated with Lugol's solution followed by 1: 3 sulphuric acid. No blue colour indicative of the presence of cellulose was obtained. Frozen sections were then treated with zinc chloride-potassium iodide solution, which stains cellulose violet, and with Post and Laudermilk's (1942) iodine stain for cellulose. Negative results were obtained in both cases.

Sections of the test were then left overnight in Schweitzer's reagent, which dissolves cellulose. Next morning the sections were washed and stained with Mallory's stain. The sections stained in identical fashion to control sections that had not been treated with Schweitzer's reagent. It would seem therefore that cellulose possessing staining reactions typical of those possessed by the cellulose of higher plants is absent from the test of *P. stolonifera.*

It was then found that Alcian Blue 8GS stained the fibres a deep blue and the interfibrillar material also stained slightly. Since Steedman (1950) has shown that under certain conditions this dye is specific for "mucin", sections of the test fixed in Carnoy's fluid were subjected to Hale's (1946) method for the detection of acid polysaccharide of the hyaluronic acid type. The fibres stained an intense blue and the interfibrillar material also stained positively.

Lison (1935) and Michaelis (1944) have shown that substrates which exhibit metachromatic staining with toluidine blue are esters of sulphuric acid with high molecular weight carbohydrates. Sections of the test, fixed in equal volumes of 8 per cent. basic lead acetate and 16 per cent. formalin, were stained with toluidine blue following the method of Sylvén (1941). The fibres became purplish red, indicating the presence of polysaccharide sulphate compounds.

Confirmation of the presence of such compounds was sought by taking sections of the test fixed in formalin-lead acetate and sections fixed in Carnoy's fluid and incubating them overnight at 37°C with 0.01 per cent. bovine testicular hyaluronidase ("Hyalase", a product of Benger's Ltd., was used), washing them, and staining for polysaccharide sulphate and acid polysaccharide respectively. In no case was any staining observed after the hyaluronidase treatment, although it was ascertained by using the phase contrast microscope that fibres were still present in the sections. The fibres, however, were disordered and much diffuse granular material was evident between them.

As has been pointed out by several workers, including Meyer (1947) and Wyburn and Bacsich (1951), the action of hyaluronidase is not specific for hyaluronic acid, as the enzyme can break down sulphate-containing mucopolysaccharides.

Pieces of test were boiled with 6N hydrochloric acid for 6 hr, washed, sectioned, and stained with toluidine blue. The fibres did not stain metachromatically and apparently the mucopolysaccharide material had been hydrolysed by the acid. However, phase contrast examination revealed that disarrayed fibres were still present. These stained with Weigert's fuchsin, though not as strongly as they did before treatment with acid. Negative results were obtained when these sections were stained for protein by the methods of Serra (1944) and Mazia, Brewer, and Alfert (1953). However, they stained positively for polysaccharide, though not as strongly as before boiling with acid, when the method of Hotchkiss (1948) was used.

Sections boiled with 6N hydrochloric acid were stained for cellulose and chitin following the methods of Zander (1897) and Bethe (1895). Negative results were obtained.

(*b*) *Epidermal Cells Lining Blood-vessels*

These stained positively for proteins and polysaccharides using the methods outlined previously. However, the staining was uniform and there appeared to be no accumulations of either of these constituents in any region of the cell. The cells did not stain with Alcian Blue 8GS and did not exhibit metachromasy with toluidine blue, and therefore presumably do not contain test material or its immediate precursor. There was also no evidence of any secretion being produced on the outer borders of the cells. Hence it is unlikely that these cells have an active role in the production of test material.

VI. CHEMISTRY OF THE TEST

(*a*) *Plasma Content*

If pieces of the gelatinous test were allowed to stand in a beaker an exudate began to accumulate in the bottom of the beaker. Initially this had a low chloride content but this increased as more fluid passed from the test. If the pieces of test were subjected to pressure until as much fluid as possible was forced out of the test, the final chloride concentration of the fluid was then found to be equivalent to that of the blood plasma. Moreover the concentrations of sulphate and cations in the test fluid were identical with those of the blood plasma (see Endean 1955). Presumably the dissolved ions are held by stronger forces to the test substance than are the water molecules.

The approximate amount of plasma present in three 50-g lots of test material was estimated as follows.

The weighed test was minced and as much fluid as possible removed by applying pressure to the minced test; the fluid was filtered off, and 200 ml of acetone was added to the test residue and allowed to stand in contact with this for 24 hr; the acetone was then filtered off, fresh acetone added, and the mixture again allowed to stand. This procedure was repeated with two further lots of acetone and the test residue was dried at 104°C until constant weight was obtained. Results were:

Sample	Loss of Weight (g)	Plasma in Test (%)
1	48.63	97.26
2	48.76	97.52
3	48.68	97.36

Assuming that the loss of weight observed was due solely to loss of plasma, it can be calculated that plasma would constitute about 97.4 per cent. of the weight of the test.

In order to check that this approximation was of a reasonable order of accuracy three 50-g lots of test were dried to constant weight at 104°C. Results were:

Sample	Loss of Weight (g)	Water in Test (%)
1	47.38	94.75
2	47.22	94.44
3	47.26	94.52

The average percentage of water in the test would therefore approximate 94.6 per cent. Since the plasma has a salinity of about 3.5 per cent. (see Endean 1955) then the amount of plasma present in the test would approximate 97.8 per cent., which is in good agreement with the value of 97.4 per cent. obtained above.

Thus the test has a markedly high water content, resembling the mesogloea of jellyfish in this respect (Lowndes 1942; Chapman 1953).

(b) *Action of Certain Reagents on Test Substance*

When boiled with water pieces of the test became slightly transparent but there was no obvious swelling or disintegration. Pieces of the test were apparently unaffected by the action of alcohol, acetone, dilute and concentrated sodium hydroxide, dilute and concentrated hydrochloric acid, dilute sulphuric acid, 6M urea, 2M calcium chloride, and 30 per cent. hydrogen peroxide. Concentrated nitric acid turned pieces of the test slightly yellowish but they did not dissolve. However, cold concentrated sulphuric acid rapidly dissolved pieces of the test.

(*c*) *Hydrolysis of the Test*

Pieces of the test totalling 50 g were minced and as much plasma as possible removed by applying pressure to the minced test. The plasma was then filtered off and 200 ml of acetone added to the test residue. After 24 hr the acetone was filtered off and fresh acetone added. After another 24 hr this was filtered off, and the residue dried and then subjected to hydrolysis with 6N hydrochloric acid for 8 hr. Disintegration of the test material was slight and the residue was filtered off, washed, dried, and retained for subsequent analysis. The hydrochloric acid, together with any hydrolysed material that it might contain, was placed in crucibles over solid sodium hydroxide in an evacuated desiccator. The residue after removal of hydrochloric acid was dissolved in a little water. This material gave a positive Molisch reaction, and gave a positive result when tested for hexosamine following the procedure of Elson and Morgan (1933).

(*d*) *Chemical Composition of the Fibres*

Because of the fibrous nature of the test and its insolubility in most of the reagents used (see Section VI(*b*)) it was considered that the structural basis of the test was composed of either a very insoluble protein or an insoluble polysaccharide. Pieces of dried test material retained after plasma, acetone-soluble material, and mucopolysaccharide material had been removed as outlined in Section VI(*c*) were used in the following investigations.

Pieces of this material were boiled with distilled water to which a few drops of Millon's reagent in one case and a few drops of 0.1 per cent. ninhydrin in another were added. Negative results were obtained, indicating the absence of protein. Pieces placed in 0.5 per cent. pepsin (pH 1.8) for 24 hr appeared unaltered. Keratin type proteins containing S-S bonds did not appear to be present, as the material was insoluble in alkaline sodium sulphide and in alkaline thioglycollate solution (Goddard and Michaelis 1934).

The material was apparently unaffected after standing in contact with Cross and Bevan's zinc chloride-hydrochloric acid reagent and with Schweitzer's reagent for 48 hr in each case. Subsequent dilution and acidification of the Schweitzer's reagent failed to produce any precipitate of cellulose.

Professor N. Lahey of the Chemistry Department, University of Queensland, obtained carbon 40.7 per cent., hydrogen 6.2 per cent. from an elementary analysis on the material. There was a residue which probably consisted of fine grains of sand as these were present in varying amounts throughout the test of all specimens examined. The results obtained indicate that the basic fibrillar material is a polysaccharide.

The results described in this Section are in conformity with those obtained using histochemical methods. It would appear that the fibres consist of a very insoluble and chemically resistant polysaccharide which does not exhibit the usual properties of the cellulose of higher plants. The chemical nature of the polysaccharide will be investigated and the presence or absence of poly-β-1:4-glucosan chains determined. The polysaccharide fibres are associated with a mucopolysaccharide.

VII. Discussion

The test of ascidians varies both structurally and functionally. In those compound ascidians that have been studied it takes the form of a "conjunctif commun", and as well as acting as a support for the ascidiozoids provides a medium through which metabolites pass from one individual to another. In the simple ascidians it takes the form of a resilient yet protective envelope surrounding the soft bodies of these animals. The thickness of this envelope varies greatly from species to species.

Saint-Hilaire (1931) has shown that the outer part of the test of many ascidians differs in some respects from the bulk of the test, and he terms this outer region the cuticle. Spicules are present in the tests of many species. Pérès (1945) remarks that in some the test is a formation "en dehors de l'organisme" and that the cells which are present there are generally cells that have been eliminated by the organism and are degenerating. He then states that "au contraire chez les deux Didemnidae étudiés et probablement chez la plupart des autres Synascidies, la tunique est un tissue bien vivant". These statements imply that he believes the tests of many simple ascidians to be effectively non-living structures. On the other hand, the tests of simple ascidians are permeated by blood-vessels and contain numerous blood cells. The presence of these may be vital for the maintenance of the structural integrity of the tests and, if so, then the test must be regarded as a living tissue.

That this is the case in *P. stolonifera* will be shown in Part III of this series. In this species the test is extremely well developed. There is no cuticle comparable to that possessed by members of the Ascidiidae, nor are spicules found in this species. However, the outer surface of the test is covered by a layer of embedded sand grains which undoubtedly protects the bulk of the test from mechanical damage by abrasive particles present in the water. Also, it affords protection against predatory animals, as evidenced by the following observations. Pieces of the tests of some specimens of the rocky ocean form were cut out so as to expose portions of the fleshy parts of the animals. Crabs (*Leptograpsus variegatus* Fabricius), which swarm over the intertidal rocks when the tide is ebbing, were observed to attack the exposed flesh and to begin devouring the animals. Moreover, many specimens attain a large size and on the basis of observed rates of growth must have been growing for some years in areas where predatory fish and crabs abound. The fact that fishermen regard the fleshy part of *P. stolonifera*, or "cunjevoi" as it is known to them, as one of the best baits for attracting these predatory animals bears witness to the efficiency of the test as a protective structure. Indeed, the only instances where predators were observed to attack specimens with intact tests occurred at Port Hacking. Large rays were observed to crush the tests of the estuarine form in the vicinity of the siphons and thus gain access to the soft parts of the animal.

The role of the test in attaching both forms to the substratum has already been commented on. Hence the test is of great importance in the economy of the animal, and in the rocky shore form must be a major factor in enabling it to dominate a niche on the sea-shore which is particularly susceptible to the battering action of the surf.

Saint-Hilaire (1931) draws attention to the similarity between the histological appearance of the ascidian test and that of vertebrate connective tissue. In both cases there are cells present in a groundmass which is enmeshed by fibres. However, there is much variation in the ratio of groundmass to fibre material from species to species in ascidians. Thus according to Saint-Hilaire (1931) some species such as *Ascidia mentula* have a cartilaginous test in which there is much more groundmass than fibres, whilst other species such as *Pyura papillosa* have a membranous test in which fibrous material predominates over groundmass. There is also a great diversity in the numbers and types of cells present in the groundmass. Pérès (1945) observes that there are more cells present in the test of compound ascidians than in that of simple ascidians. In some species of the Didemnidae he has shown that the cells present in the test form a cellular reticulum.

In the test of *Pyura stolonifera* there is a prominent network of fine fibres which vary in diameter from 0.3 to 0.5 μ but become aggregated in certain regions to form larger fibres. Probably the fine fibres themselves are aggregates of still finer fibrils. The interfibrillar material exhibits no obvious structure and is mainly fluid, the test containing over 90 per cent. of water. This fluid, which can be removed from the test by applying pressure, has the same inorganic composition as the blood plasma, with which it must be in dynamic equilibrium.

Large numbers of ferrocytes, some wandering about in amoeboid fashion, some stationary, are found amongst the fibres. These cells enter the test substance by migrating across the walls of the blood-vessels which run through the test.

In some species of ascidians Saint-Hilaire (1931) has found that the fibres stain with resorcin, fuchsin, and orcein in a manner similar to the elastic fibres of vertebrate connective tissue. In other species the fibres behave otherwise. He has also shown that the fibres are richer in nitrogen-containing material than the groundmass, although he states both fibres and groundmass contain tunicin. Pérès (1948*a*) has shown, using histochemical techniques, that the test of *Clavelina lepadiformis* contains tunicin and stains metachromatically with toluidine blue. This metachromasy he believes to be due not to cellulose but to the "protéides accompagnant en faible proportion celle-ci et qui peuvent être considérés comme des glycoprotéides".

The test fibres of *P. stolonifera* stain positively for polysaccharide and metachromatically with toluidine blue. With fuchsin and orcein they stain in a manner which has been assumed specific for the collagen fibres found in vertebrate tissues. After treatment with hyaluronidase or 6N hydrochloric acid the fibres still contain polysaccharide but no longer exhibit the metachromasy with toluidine blue specific for mucopolysaccharide. As no definite protein reaction was obtained either before or after treatment, the specificity of orcein and fuchsin for collagen is evidently questionable.

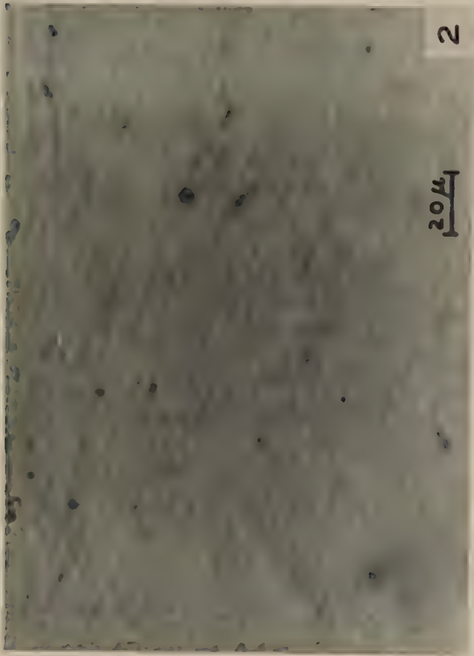
The presence of a cellulosic material in ascidians was first shown by Schmidt (1845) and the substance was subsequently termed tunicin by Berthelot (1858). In all species so far investigated it seems to be chemically identical with plant cellulose (Winterstein 1894; Abderhalden and Zemplén 1911; Saint-Hilaire 1931). X-ray diffraction studies have been made on a few species and diffraction patterns similar to those given by plant cellulose were obtained (Herzog and Gonell 1924; Meyer and Mark 1930; Spence and Richards 1940). However, the chemical composition of the tests of the majority of ascidian species has not been investigated, and it is possible that some may contain structural material which is not identical with plant cellulose.

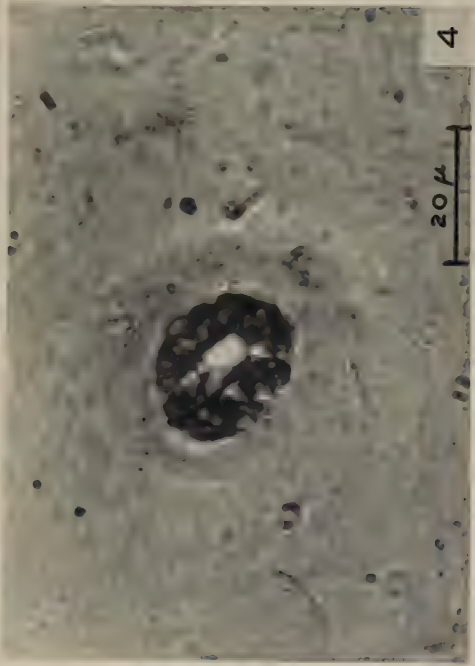
The fibrillar material of *P. stolonifera*, after mucopolysaccharide material which stains metachromatically has been removed, is polysaccharide in nature as evidenced by staining reactions and elementary analysis. It behaves similarly to cellulose in being insoluble in most ordinary solvents but soluble in concentrated sulphuric acid. However, it will not dissolve in special cellulose solvents such as Schweitzer's reagent or zinc chloride-hydrochloric acid solution, nor will it stain with the usual cellulose stains. Its molecular architecture must differ therefore from that of plant cellulose.

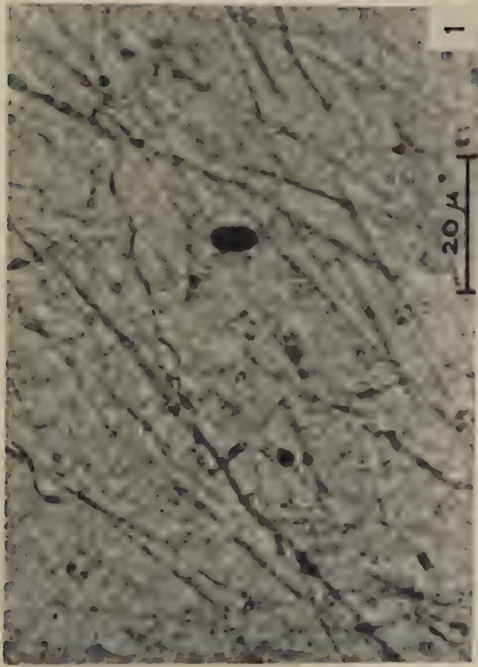
In vertebrate connective tissues there are fibrillar components (mainly collagen fibrils) embedded in a groundmass. Hyaluronic acid constitutes the bulk of the groundmass, and another mucopolysaccharide, chondroitin sulphuric acid, seems to cement the fibrils together (Meyer and Smyth 1937; Meyer and Chaffee 1941). Meyer (1947) states that hyaluronic acid is "a mucopolysaccharide acid which in animal tissues seems to bind water in interstitial spaces. It further holds cells together in a jellylike matrix and serves as a lubricant and shock absorber in joints". There is, however, little information on the manner in which chondroitin sulphuric acid and collagen are linked. Partridge (1948) and Jackson (1953) both suggest that chondroitin sulphuric acid may be taking part in the intermolecular linking of the collagenous fibres.

In the test of *P. stolonifera* the fibrils are composed of a very insoluble polysaccharide associated with a mucopolysaccharide. The mucopoly-

BLOOD AND TESTS OF AUSTRALIAN ASCIDIANS. II







saccharide material, as evidenced by histochemical staining, appears to be concentrated on the fibrils but there is some present in the interfibrillar spaces. The concentration of materials in these spaces, however, must be slight because of the high water content of the test (over 90 per cent.). Possibly the mucopolysaccharide present there binds water to a certain extent. By analogy with the suggested function of mucopolysaccharide associated with the protein fibres of vertebrate connective tissue, the mucopolysaccharide material associated with the polysaccharide fibres of ascidian tests might function as a cementing agent. The fact that after treatment with hyaluronidase the fibres in the test of *P. stolonifera* become disorganized seems to support this hypothesis.

VIII. ACKNOWLEDGMENTS

The author is indebted to Professor W. Stephenson of the University of Queensland for reading and discussing the manuscript, and to Professor N. Lahey of the University of Queensland for carrying out an elementary analysis on the polysaccharide material.

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EXPLANATION OF PLATE 1

All photographs are of 10-μ sections

Fig. 1.—Section stained with orcein showing interlacing fibres of varying size. Blood cells are in evidence between the fibres.

Fig. 2.—Section stained with orcein showing fibres orientated predominantly in one direction. Blood cells are present between the fibres.

Fig. 3.—Section stained with Mallory's stain showing a small blood-vessel in longitudinal section and fibres in the immediate vicinity running parallel to its course.

Fig. 4.—Section stained with orcein showing small blood-vessel in transverse section and fibres running concentrically around it.

STUDIES OF THE BLOOD AND TESTS OF SOME AUSTRALIAN ASCIDIANS

III. THE FORMATION OF THE TEST OF PYURA STOLONIFERA (HELLER)

By R. Endean*

(*Manuscript received October* 27, 1954)

Summary

Certain blood cells, termed ferrocytes, produce fibres when cytolysed. Similar fibres may be produced by these corpuscles when kept in "hanging drop" preparations. In both cases histological and histochemical examination shows that the fibres are identical with those present in the test.

Under normal conditions ferrocytes migrate across the walls of blood-vessels and enter the test substance. After moving about for a time amongst the fibrillar matrix already deposited, they produce fibres by one of three methods:

(i) A cytoplasmic centre, from which fibres subsequently arise, may be isolated from the main corpuscular mass.
(ii) Fibres may arise directly from the surface of the ferrocyte.
(iii) Fibres may arise from material secreted by the ferrocyte into its immediate vicinity.

In many respects the process of test fibre formation resembles the production of vertebrate connective tissue fibres from fibroblasts.

During regeneration of the test, ferrocytes migrate straight to the test—sea-water interface and there produce fibres, seemingly as a direct result of the release of fibre-producing intraglobular material on cytolysis. The probable mode of formation of the tough outer test is also discussed.

I. Introduction

Despite the interest aroused by the discovery of tunicin in the ascidian test, the origin of this tunicin and the mode of formation of the test itself is little understood. Brien (1930) removed part of the test of *Clavelina lepadiformis* (Müller) and studied its regeneration. He found that the tunic was regenerated only in the vicinity of epidermal cells, but noted that while the tunic was being formed there was a great migration of vacuolated cells from the blood spaces across the epidermis to the region of test formation. These observations led him to pose the question "est-il (the epidermis) l'agent initial ou un intermédiare à travers lequel diffuse la substance destinée à former au contact de l'eau la tunique vraie?".

Saint-Hilaire (1931) believed that tunicin-forming material passed through intercellular spaces in the epidermis. Pérès (1948*a*, 1948*b*) found no evidence for such a passage of test-forming material in *Clavelina lepadiformis* and *Ciona intestinalis* L., although he believed that the epidermal cells played the major role in the secretion of the test. He

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maintained that, in the two species mentioned, the epidermal cells themselves take up tunicin-forming materials from the blood which they then pass to the exterior where polymerization of these substances occurs, resulting in test formation.

In the Didemnidae, Millar (1951) has shown that the terminal epidermal cells of the stolonic vessels of some species secrete material which he interprets as an area of test substance "into which cells and fibres have not yet penetrated". However, in *Lissoclinum argyllense* Millar, another of the species he investigated, no secretion arising from the stolon was observed. Instead a strand or tuft of strands connected the apical border of each epidermal cell to the common test. According to Millar this phenomenon resembles a process which has been termed "tunicization" by Pérès and which was observed by Pérès to occur in some species of the Didemnidae. This "tunicization" involves a transformation of the outer borders of the epidermal cells.

It would appear then, from the evidence available, that the epidermal cells play the principal part in test secretion, although the actual mode of formation may vary from species to species. On the other hand, both Saint-Hilaire (1931) and Pérès (1948*a*) have noted that mesenchyme cells from the blood migrate into the test and occasionally participate in the formation of test substance. According to Pérès this method of test production is exceptional, although he believed the cuticle—the thin outer layer of the test—to be formed solely in this manner.

In a previous paper (Endean 1955*b*), it has been shown that there is an abundance of blood-vessels with an epidermal lining in the test of *Pyura stolonifera* and also that there are large numbers of blood cells of the ferrocyte category (Endean 1955*a*) wandering about in the substance of the test. This paper records the results of investigations made on the formation of the test which throw light on the respective roles of the epidermal cells lining the blood-vessels and the immigrant blood cells of the test.

II. Materials and Methods

As in previous investigations ascidians belonging to the two environmental forms of *P. stolonifera* were used. The rocky ocean shore form was obtained from Maroubra Bay, N.S.W., and subsequently from Currumbin, Qld., whilst the estuarine form was obtained from Port Hacking, N.S.W. Descriptions and drawings of these forms are given in previous papers of this series.

The methods used in this investigation are described under relevant headings.

III. The Production of Fibres by Ferrocytes

During the histological investigations made on the blood of *P. stolonifera*, fibres were frequently observed amongst blood corpuscles which had been placed on slides. It was thought at first that these fibres were merely foreign bodies. Precautions were then taken to ensure that the slides were perfectly clean and that the blood placed on the slide was not exposed to contamination by airborne particles. However, fibres were still observed amongst the blood corpuscles, and it was then discovered that the number of fibres present was related to the length of time that the blood had stood prior to examination and hence on the number of cells that had cytolysed.

Corpuscles, separated by centrifugation from the plasma, were placed on slides, flooded with distilled water, and examined by phase contrast microscopy. Cytolysis of the cells soon occurred. Frequently the globules present in ferrocytes were liberated on cytolysis. When the globules themselves burst, the intraglobular material, which consisted of numerous granules suspended in a fine slime, poured forth to form a matrix. In this matrix condensations in the form of fine wavy lines appeared in many cases. Hyaline filamentous processes were seen to originate almost immediately in these areas, and these processes shot out across the surface of the slide, interlacing repeatedly with one another. A small quantity of intraglobular material was dragged out with each process. Each filamentous process then gradually assumed a definite fibre form and granules in a state of violent agitation were observed along the length of the longer fibres. As the fibres lengthened the quantity of intraglobular material from which each had arisen was progressively diminished. Some of the fibres were relatively long (up to 200 μ) and had diameters of the order of 0.3-0.5 μ (Plate 1, Figs. 1 and 2).

The fibres stained metachromatically with toluidine blue, were positive to the polysaccharide stain of Hotchkiss (1948), and stained with a variety of other histochemical reagents and stains in exactly the same way as the fibres of the gelatinous test (see Endean 1955*b*). Undoubtedly they are identical with these, but the observations to be described below suggest that fibre production *in vivo* involves more than just a cytolysis of ferrocytes.

As yet it has not been possible to determine the stimulus or stimuli normally responsible for the initiation of fibre production by ferrocytes. "Hanging drop" preparations of living blood cells enabled ferrocytes to be kept alive for over 24 hr. Some of the ferrocytes present in these preparations were observed to cease pseudopodial activity and to put out a thread-like protoplasmic extension which had a terminal knob in which granules undergoing violent movement were observed. The contours of each knob changed frequently owing to nodular portions of protoplasm being alternately protracted and retracted from the surface. In a few cases thick fibres pushed out from these protoplasmic knobs (Plate 1, Fig. 3). As the fibres increased in length there was a concomitant decrease in the quantity of intracellular material present in each ferrocyte.

IV. Fibre Production in the Test

In sections of the test of *P. stolonifera*, fixed with Susa and Bouin's fluids and stained with azan stain, ferrocytes with protoplasmic extensions similar to those described above were observed. From one to many fine fibres radiated out in random fashion from many of the terminal knobs of these extensions (Plate 1, Fig. 4, and Plate 2, Fig. 5). Refractile granules could often be seen both in the cytoplasmic knob itself and also at the base of the protoplasmic extension which connected the knob to the cell from which it had arisen. Such cells were frequently elongated, sometimes spindle-shaped, and in various stages of degeneration, as evidenced by the reduction in the number of globules normally present in such cells. In some cases the terminal protoplasmic knobs had broken away from the cells that had formed them.

It would appear that fibres can also arise directly from the cell surface without the protrusion of a protoplasmic centre of fibre formation (Plate 2, Figs. 6 and 7). Fibres that had arisen in such a way sometimes pursued fairly straight courses (for distances up to 150 μ from the cell), sometimes they forked, and usually granules were observed along the course of these fibres. Again the cells that had given rise to such fibres were in various stages of degeneration and sometimes only fragments remained.

In other cases fibres had arisen from a darkly staining region or regions near a ferrocyte or between two adjacent cells. Such a centre frequently had a wavy appearance and fibres radiated out in all directions from it (Plate 2, Fig. 8). Sometimes refractile bodies could be observed at or near the centre of fibre formation but at other times these bodies were absent.

It is noteworthy that fibre formation as it appears to occur in the test of *P. stolonifera* bears a marked resemblance in some respects, particularly in the isolation of a protoplasmic centre of fibre formation, to the formation of vertebrate connective tissue fibres from fibroblasts as described by Stearns (1940).

V. TEST REGENERATION

Small wedge-shaped pieces (about 1 cm long, 0.5 cm wide at the base, and about 1 cm deep) were cut out of the peripheral region of the test of fresh specimens of *P. stolonifera* and the specimens placed in a tank of oxygenated sea-water. Some were taken from the tank after 24 hr and others after 48 hr. The regions of the tests in the immediate vicinity of the areas where the V-shaped pieces had been removed were then cut out in such a way as to contain any test that might have regenerated. These portions of the tests were fixed in Susa and Bouin's fluids, sectioned at 10 μ, stained with Mann's eosin-methyl blue, and examined.

All sections revealed a great migration of ferrocytes across the walls of the blood-vessels, near the region where the excision had been made and towards this region. This was particularly well marked in the earlier regenerates, but was still in progress in the sections from specimens in which regeneration had been allowed to occur for 48 hr. In the latter the regenerated test averaged 100 μ in thickness and in a few cases blood-vessels had already begun to penetrate this area. The original surface of the test where each excision had been made was revealed as a dark blue line, stained by the methyl blue component of the stain. The edge of the regenerating test was stained red by the eosin component and it was here that the ferrocytes had aggregated in large numbers (Plate 3, Figs. 9 and 10). Many of them had cytolysed, apparently as a result of contact with sea-water, and the red staining observed in this region was due to the liberated intracorpuscular material. Much of this material had given rise to and was enmeshed by a network of fibres. Between the original cut surface and the aggregated ferrocytes, fibres which stained blue were observed. These were orientated predominantly in a direction parallel to the nearest surface of the original test. Ferrocytes were observed amongst these orientated fibres but only a few were producing fibres and few degenerating cells were observed. This would seem to indicate that the majority were moving towards the test-water interface where the ferrocytes were aggregated, and that it is here that the bulk of fibres are deposited. Presumably there is some rearrangement of the fibres after they have been formed in this region. In this region too, much detritus had been caught up in the material exuded from the cytolysed cells and this suggests the manner in which the external coating of the test of the present species is formed.

Ten adult specimens of the estuarine form were uprooted and the bottom third of the test (bearing the long roots) removed by a transverse cut. In each case a point on the ridge which surrounds the base of the siphons was then taken as a reference point and the distance to the cut surface of the test noted. The animals were then returned to their original holes and sand packed tightly around them. Six survivors were pulled up and examined after a period of 9 weeks. Measurements of the amounts of regeneration were complicated by the fact that the outer edge of the original cut surface appeared to have grown more rapidly, causing this region to curl inwards slightly. This was due apparently largely to a greater accumulation of foreign bodies—sand grains, foraminiferan skeletons, and fragments of mollusc shells—in this region. Increases in length of 0.7-1.2 cm had taken place (Plate 3, Fig. 11). In some cases a few of the characteristic root-like extensions of the test had appeared.

VI. Discussion

From the evidence available it would seem that the structure and to some extent the chemical composition of the ascidian test varies from species to species. There is also variation in the mode of formation of the test (Saint-Hilaire 1931; Pérès 1945, 1948*a*, 1948*b*; Millar 1951). However, in previous cases the epidermis appears to play the principal role in test formation. In Part I of this series (Endean 1955*a*) it was shown that there are present in the blood of *P. stolonifera* large numbers of morula-shaped cells which carry an iron compound in association with aminopolysaccharide material. These cells were termed ferrocytes and their mode of formation from the primitive lymphocytes of the blood was described.

In Part II (Endean 1955*b*) the structure and chemical nature of the test of *P. stolonifera* was investigated. It was shown that the bulky gelatinous portion of the test had a markedly high plasma content, the plasma being held in the interstices of a fibrillar matrix. The fibres consisted of two components—an unidentified very insoluble fibrous polysaccharide and, associated with this, an aminopolysaccharide which was responsible for the metachromasy exhibited by the fibres of the test.

Blood-vessels with a lining of cubical epidermal cells coursed through the test, and ferrocytes, moving in amoeboid fashion between the fibres, were present in abundance. The ferrocytes had entered the test by passing through the epidermal cells lining the blood-vessels. There was no accumulation of possible test-forming material inside these epidermal cells, nor was there any evidence of any secretion being produced by these cells. Hence they can play no active role in test formation in *P. stolonifera*. This conclusion is contrary to the position found in other species of ascidians examined, where the epidermal cells play a prominent part in test formation (Saint-Hilaire 1931; Pérès 1945, 1948*a*, 1948*b*; Millar 1951).

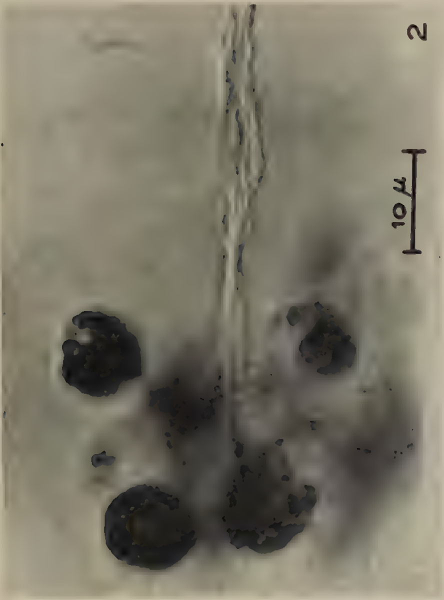
In the present paper it has been shown that fibres with histological and histochemical properties identical with those possessed by the fibres of the test can arise from the intraglobular material of ferrocytes on cytolysis of these cells and also from spatulate processes put out by ferrocytes kept in "hanging drop" preparations.

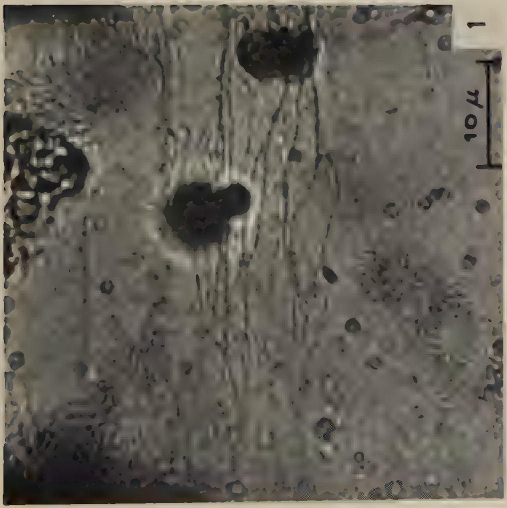
Precursors of the fibrillar material first appear during the formation of ferrocytes from lymphocytes at the "signet ring" stage. At this stage there is great intracellular activity (see Endean 1955*a*). These substances are further elaborated during subsequent stages of development. Some stimulus (or stimuli), as yet not determined, causes the fully developed ferrocytes to migrate through the epidermal cells lining the blood-vessels and to enter the gelatinous test. Here they wander about amongst the fibres until another stimulus or set of stimuli causes them to cease movement and to produce fibres. Fibres can arise in three different ways: (i) directly from the cell surface of a ferrocyte; (ii) from a cytoplasmic knob pushed out from a ferrocyte; (iii) from material released into its immediate environment by a ferrocyte. In all cases the ferrocytes subsequently degenerate.

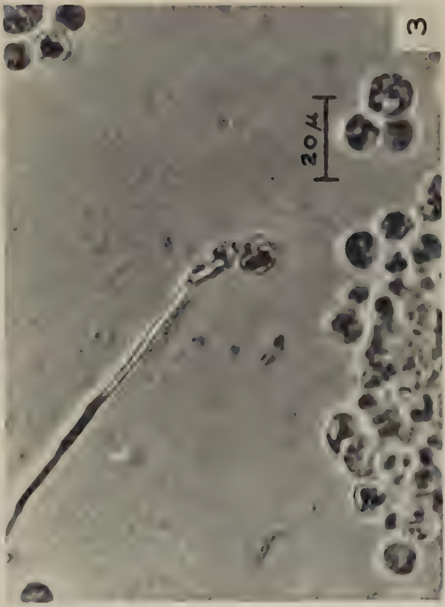
Fibres produced in the above ways are continually being deposited during the life of the animal, and cause a constant increase in the bulk of the test. Moreover, the region of attachment to the substratum is continually being strengthened and increased in area as a result of deposition of fibres there.

If the test is damaged, regeneration is rapid. Ferrocytes migrate in large numbers towards the damaged region. In this case, however, these

BLOOD AND TESTS OF AUSTRALIAN ASCIDIANS. III







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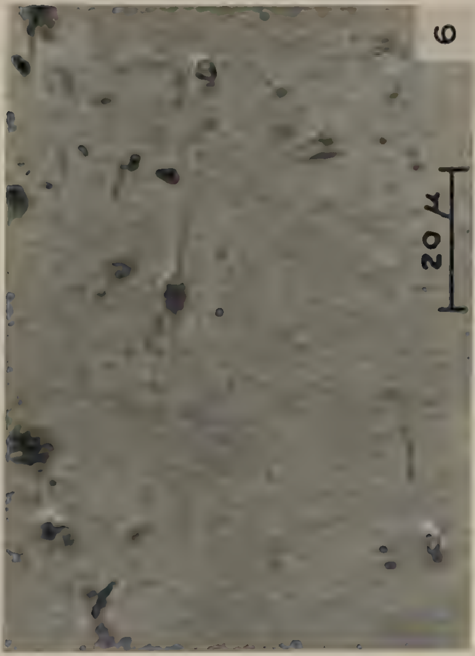

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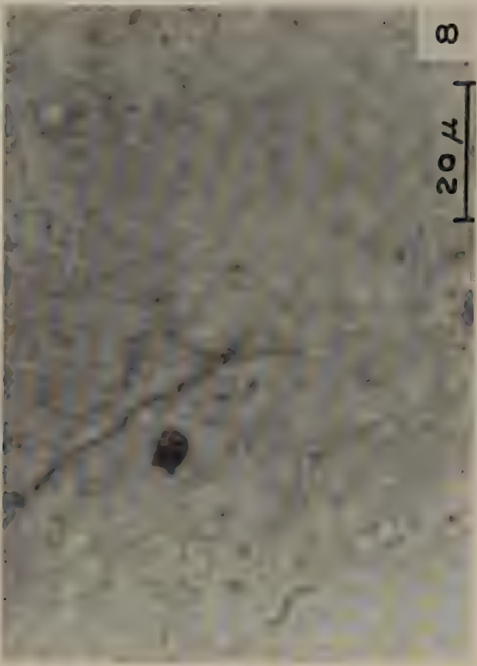

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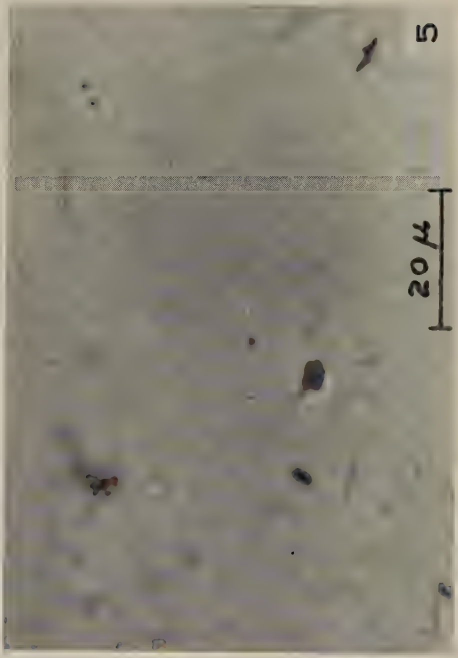

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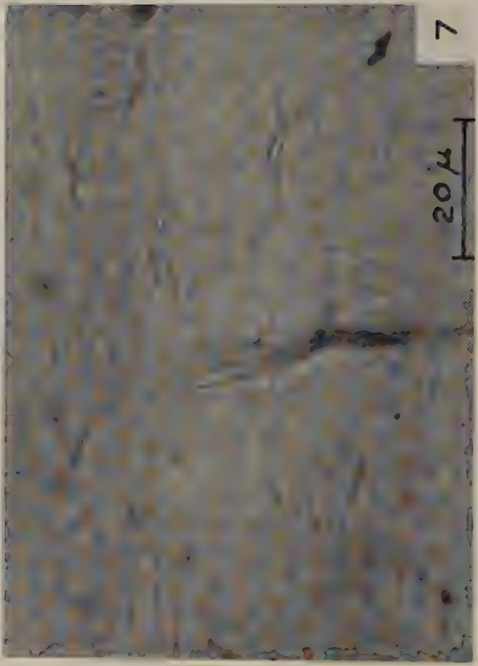
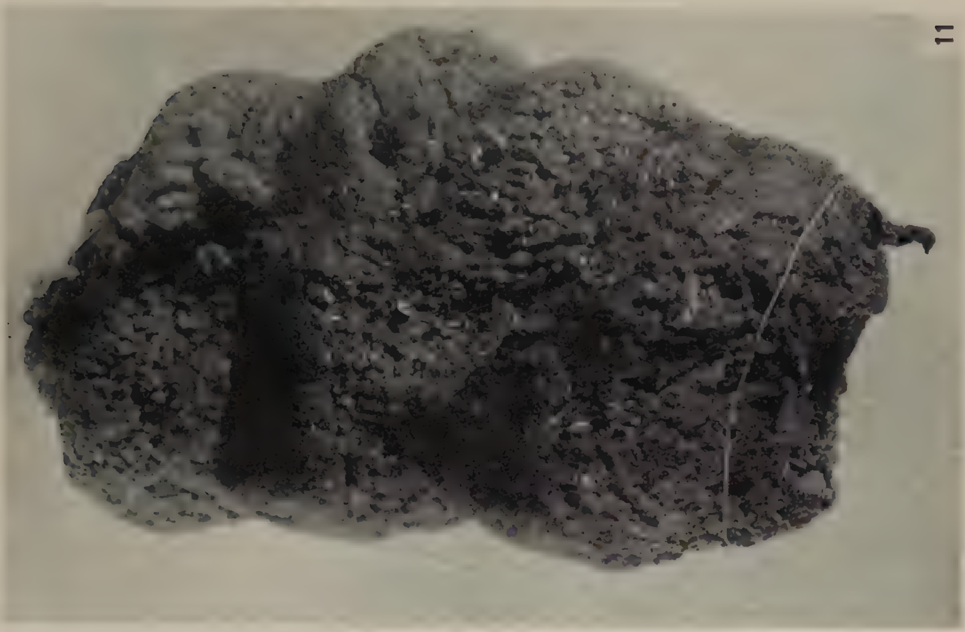
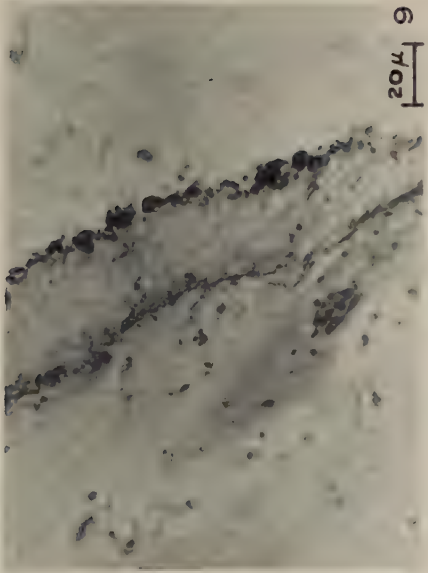
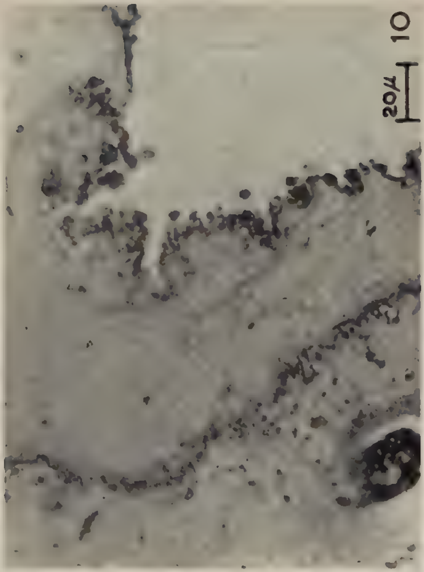


7

BLOOD AND TESTS OF AUSTRALIAN ASCIDIANS. III







cells proceed mainly to the test—sea-water interface and appear to be cytolysed by the sea-water, fibres arising from the released intracorpuscular material.

Thus in *P. stolonifera* the ferrocytes of the blood play the principal part in the formation and maintenance of the test. The regeneration experiments confirm the view expressed earlier (Endean 1955*b*) that the blood-vessels push through the fibre network after this has been deposited. It would seem that the role of the blood-vessels in this species is to provide a means whereby ferrocytes can be brought quickly to a region where fibres are to be deposited.

VII. ACKNOWLEDGMENTS

The author is indebted to Professor W. Stephenson of the University of Queensland for advice and for reading and discussing the manuscript, and to Professor P. D. F. Murray of the University of Sydney for helpful advice and criticism. Enlargements of the author's negatives were made by Mr. E. Hollywood, of the University of Queensland.

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EXPLANATION OF PLATES 1-3

PLATE 1

Fig. 1.—Fibres arising from cytolysing ferrocytes. Numerous liberated globules and aggregated intraglobular material are in evidence. Neutral red was added to the distilled water that is causing cytolysis. Phase contrast.

Fig. 2.—Cytolysing ferrocyte producing large fibre. Distilled water to which neutral red has been added is causing cytolysis. Phase contrast.

Fig. 3.—"Hanging drop" preparation showing ferrocyte with protoplasmic process from which a large fibre has arisen. Phase contrast.

Fig. 4.—Ferrocyte with protoplasmic process as in Fig. 3 from 10-μ section stained with Mann's eosin-methyl blue. Phase contrast.

PLATE 2

Fig. 5.—Fibres (one in focus) arising from protoplasmic process extruded by ferrocyte. From a 10-μ section stained with Mann's eosin-methyl blue. Phase contrast.

Fig. 6.—Section (10 μ) stained with Mann's eosin-methyl blue showing fibres arising directly from ferrocyte. Phase contrast.

Fig. 7.—Clump of fibres arising directly from degenerating ferrocyte. From a 10-μ section stained with orcein. Phase contrast.

Fig. 8.—Degenerating ferrocyte with clump of fibres arising from darkly staining centre nearby. From 10-μ section stained with orcein.

PLATE 3

Fig. 9.—Section (10 μ), stained with Mann's eosin-methyl blue, of portion of test where regeneration has been allowed to proceed for 48 hr. Clumps of ferrocytes can be observed at edge of newly formed test. The cut surface of the original test is denoted by a dark line. Phase contrast.

Fig. 10.—Section (10 μ), stained with Mann's eosin-methyl blue, of portion of test where regeneration has been allowed to proceed for 48 hr. Ferrocytes can be seen migrating from small blood-vessel to region where test regeneration is occurring. Phase contrast.

Fig. 11.—Specimen of estuarine form of *P. stolonifera* which has had the bottom third of the test removed. Regeneration of the test was allowed to proceed for 9 weeks. The white cotton denotes the approximate position of the original cut surface and an indication can be gained of the general manner in which regeneration has occurred.

THE NEW SOUTH WALES TRAWLFISHERY: REVIEW OF PAST COURSE AND EXAMINATION OF PRESENT CONDITION

By T. W. Houston*

(*Manuscript received November* 10, 1954)

Summary

The past course of the New South Wales mixed trawlfishery is reviewed mainly on the basis of the available catch and fishing effort statistics.

The size composition of tiger flathead landings from 1946-47 to 1953-54, and the age composition for certain post-war years, are analysed in conjunction with catch per unit effort data. The results suggest that 1943-44, 1944-45, 1947-48, and 1948-49 were relatively poor brood years, and 1945-46 and 1946-47 relatively good.

The fluctuations in availability of tiger flathead (*Neoplatycephalus macrodon* (Ogilby)) are accounted for after making certain valid assumptions. It is considered probable that the unexpectedly low catches of tiger flathead in the immediate post-war years were due to inefficiency of the few steam trawlers then working, and that Danish seiners were unable to exploit fully the available V+ and higher age-group fish.

An examination of the present situation indicates that the New South Wales stock of tiger flathead is at a low level and is likely to reach even lower levels in the future if fishing intensity remains as high as in 1953-54.

An improvement of the existing catch per unit effort would be expected if fishing intensity was reduced to the level of the middle nineteen-thirties (i.e. approx. 3500 trawler-tons).

Other regulative measures would need to be introduced to bring about an improvement in the annual catch of tiger flathead. These measures should aim at ensuring a more favourable weight-length relation.

I. INTRODUCTION

Herlihy (1927) outlines the history of the New South Wales trawlfishery for the years 1915-1924, and various stages of the course of the fishery have been traced by Colefax (1934) and Fairbridge (1948, 1952). Fairbridge, who also (1952) deals with the condition of the fishery as it was in the year 1948-49, re-emphasizes the fact that because of signs of overfishing, and especially in connexion with the New South Wales stock of tiger flathead, *Neoplatycephalus macrodon* (Ogilby), there is an urgent need for regulative measures as a means of ameliorating the depleted condition of the stocks of fish.

Owing to the untimely death early in 1950 of Mr. W. S. Fairbridge, the analysis of data relating to the New South Wales trawlfishery came to a halt and was not started again until two years later.

Recent analysis has revealed that the fishery has further deteriorated since 1948-49. It has therefore seemed worth while to document the details

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of these changes for future reference, endeavour to explain the recent course of the fishery in the light of the new material which is to hand, and draw such tentative conclusions as the limited nature of the data justifies. Some unpublished data assembled by Fairbridge have been incorporated in this paper.

II. THE FISHERY AS A WHOLE

(*a*) *General*

The New South Wales commercial trawlfishery had its beginning in the year 1915 after the five years of successful exploratory trawling investigations carried out under the direction of the late Mr. H. C. Dannevig, in the Federal Investigation Ship *Endeavour,* under commission to the Commonwealth Government. Dannevig (1913) gives a summary of some of his early pioneering work.

The fishery was managed originally by the New South Wales Government, which operated three steam trawlers. Four more vessels were later added to the fleet but owing to circumstances apparently not related to the supplies of fish (see Herlihy 1927), fishing operations ceased in February 1923. The trawling venture was taken over by private enterprise in August 1923 and the fishery subsequently expanded. The fleet was enlarged and this increase resulted in improved annual total catches. The expansion phase, as will be seen from Figure 1, continued up to 1929, when the annual total catch reached an initial peak. The annual total catch and catch per unit effort fell, however, during the period 1930-1934, and the fleet was reduced in size.

Danish seiners commenced working along the New South Wales coast in 1936 and the annual total catch, which had been increasing since 1935, reached a second peak in the financial year 1938-39.

Normal fishing operations were curtailed in 1939, and in 1940 most of the fishing vessels were taken over for wartime duties. Production decreased as a consequence and it was not until 1944-45, when the fleet was being rehabilitated, that the annual total catch again showed signs of improvement. The trend of rising catch culminated in 1946-47 with the third and highest peak of production. The following year witnessed a sharp decline in catch and the decline continued until 1951-52. The total catch figure for 1952-53 showed a slight improvement over the two previous years.

The present fleet, consisting of 10 steam trawlers and approximately 70 Danish seiners, operates within an area extending 150 miles north and 250 miles south of Sydney and out to the edge of the continental shelf. The steam trawlers also fish the grounds in Bass Strait. A general description of the trawling grounds with an accompanying chart is given by Colefax (1934).

At present there are two steam trawling companies based on the port of Sydney, where all trawler catches are landed. The major part of each trawler catch is auctioned for sale in the Sydney Fish Market, and the rest (about 15 per cent.) is sold by the trawler owners direct from their wharves.

The Danish seiners, working mainly from the ports of Newcastle, Sydney, Wollongong, Ulladulla, and Eden, mostly fish the grounds close to their home ports but occasionally move up and down the coast according to reports of availability of fish. Their catches are landed at the various ports along the coast, and most of them are subsequently transported by road to the Sydney Fish Market for sale and distribution.

To give some idea of the present day relative importance of trawled fish (including landings from Danish seiners) to the New South Wales annual total fish production, the following data were extracted from the New South Wales Fisheries Branch's Annual Report for the year 1951-52.*

Fish Production	lb	Fish Imports	lb
Trawled catch	11,100,259	Frozen, smoked, dried, or potted	12,064,534
Extra-territorial catch (using traps and hand lines)	3,501,398		
Inshore catch (estuarine)	10,159,355	Canned	10,607,978
Inland catch	711,498		
	25,472,510		22,672,512

Tiger flathead (*Neoplatycephalus macrodon*), morwong (*Nemadactylus macropterus* (Bloch & Schneider)), and nannygai (*Trachichthodes affinis* (Günther)) are the three main species taken on the trawlfishing grounds; only the vernacular names are used hereafter.

(*b*) *Source of Catch and Effort Statistics*

A detailed and critical account of the origin of the catch data and methods involved in deriving the fishing effort statistics, relating to this fishery, is given by Fairbridge (1948). For the present paper only a brief summary is necessary.

Except where otherwise stated, the catch figures have been assembled from data given by Herlihy (1927) and the Annual Reports of the New South Wales Fisheries Branch, and from information supplied by the Maritime Services Board of New South Wales (earlier known as the Sydney Harbour Trust).

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* At the time of writing comparable data for 1952-53 and 1953-54 had not been published.

In attempting to account for the present condition of the fishery it is essential to have knowledge of the fishing intensity of previous years. For this purpose the fishing effort of the steam trawlers has been somewhat roughly assessed as the gross tonnage of trawlers operating in each year.

A more reliable index of the condition of the fish stocks would have resulted if data had been available on catch per hour's fishing or catch per day's absence. Unfortunately, owing to the lack of such information it was found necessary to use a less sensitive measure of availability, namely, the catch per trawler-ton. As will be seen later, there are definite limitations to the usefulness of this index.

So far the comparative efficiencies of the steam trawler and the Danish seiner, with their respective gears, have not been tested in these waters. The Danish seiners, however, have been included in the total fishing effort statistics by taking one of these vessels as equivalent to 30 trawler-tons. This conversion factor was calculated from a few individual catch returns and used successfully by Fairbridge (1948, 1952).

The statistics subsequently derived by using the trawler-ton as the measure of fishing effort are not to be regarded as ideal or in any way exact, but they are the only ones available which give a reasonable general picture covering almost the whole of the period the fishery has been operating.

It must be mentioned that the values for catch and fishing effort presented here are not in entire agreement with those given by Fairbridge (1948, 1952). A few minor corrections were made after consulting the original material.

(*c*) *Total Landings from the Combined Fleets*

The statistics on total catch and total fishing effort for the combined steam trawler and Danish seiner fleets are assembled in Table 1.

Annual landed catches were low in the early years mainly owing to the small size of the fleet, but also in part as a result of the limited market for trawled fish, and partly owing to the technical difficulties—not the least of which was the finding of workable trawling grounds—normally associated with the development of a new trawlfishery. The catch per unit effort figures for the years 1915-16 to 1922-23 were therefore omitted from Table 1, as in all probability they would have given erroneous indications of the availability of fish on the grounds in those years. The fishing effort totals for the years 1937-38 to 1942-43 include only approximate figures for Danish seiners, but they were entered in Table 1 to give some indication of the period when the Danish seine gear was introduced into the fishery and to show the reduction of fleet size during the early years of the war.

In the 1951-52 and 1952-53 Annual Reports of the New South Wales Fisheries Branch, Danish seiners have been credited with catches of Australian "salmon", *Arripis trutta* (Bloch & Schneider), a species of fish

TABLE 1

LANDED CATCH (ALL SPECIES), FISHING EFFORT, AND CATCH PER UNIT EFFORT (STEAM TRAWLERS AND DANISH SEINERS COMBINED)

Year	Catch (lb)	Total Fishing Effort (trawler-tons)	Catch per Trawler-ton (lb)	Catch* (lb)
1915-16	1,630,380	660		1,630,380
1916-17	1,637,070	660		1,637,070
1917-18	1,897,650	660		1,897,650
1918-19	3,023,640	660		3,023,640
1919-20	5,585,160	1100		5,585,160
1920-21	5,527,140	1540		5,527,140
1921-22	5,404,680	1540		5,404,680
1922-23 (8 months)	3,258,240	1540		3,258,240
1923 (5 months)	2,867,200			2,867,200
1924	5,302,155	1117	4747	5,302,155
1925	7,694,757	1455	5288	7,694,757
1926	8,461,600	2044	4139	8,461,600
1927	10,673,600	2294	4652	10,673,600
1928	12,785,920	2514	5085	12,785,920
1929	14,693,000	4103	3581	15,076,600*
1930	12,972,827	3883	3341	14,219,937*
1931	11,421,412	3883	2941	11,436,182*
1932	10,285,625	3683	2793	11,740,708*
1933	9,556,260	3443	2775	9,721,495*
1934	8,860,740	3443	2573	9,905,510*
1935	9,772,350	3243	3013	10,794,484*
1936	10,539,340	3243	3250	13,834,170*
1937-38	13,482,000	3717		13,716,990*
1938-39	13,870,130	3747		14,089,440*
1939-40	12,075,084	3040		12,387,144*
1940-41	7,364,130	1729		8,043,180*
1941-42	6,862,800	2132		6,862,800
1942-43	2,240,062	357		2,240,062
1943-44	2,275,550	537	4238	2,275,550
1944-45	10,069,807	1715	5872	10,069,807
1945-46	12,791,875	2743	4663	12,791,875
1946-47	16,165,102	4525	3572	16,165,102
1947-48	15,179,836	5633	2695	15,179,836
1948-49	14,152,417	4897	2890	14,152,417
1949-50	12,913,393	4717	2738	12,913,393
1950-51	11,230,164	4387	2560	11,230,164
1951-52	10,510,203†	4056	2591	10,510,203†
1952-53	12,281,042†	4776	2571	12,281,042†

* Includes landings from vessels not strictly belonging to the categories of steam trawlers or Danish seiners.

† Excludes catches of Australian "salmon" (*Arripis trutta*). See text for explanation.

which is not taken with the Danish seine gear. Adjustments of the totals given in the Reports were therefore necessary. Some Danish seine vessels are on occasions used as "carriers" for the vessels which are actually engaged in fishing for Australian "salmon", and the amounts "landed" by these Danish seiners would appear in their monthly fishing returns. These "landings" have been omitted from the catch totals given in Tables 1 and 3.

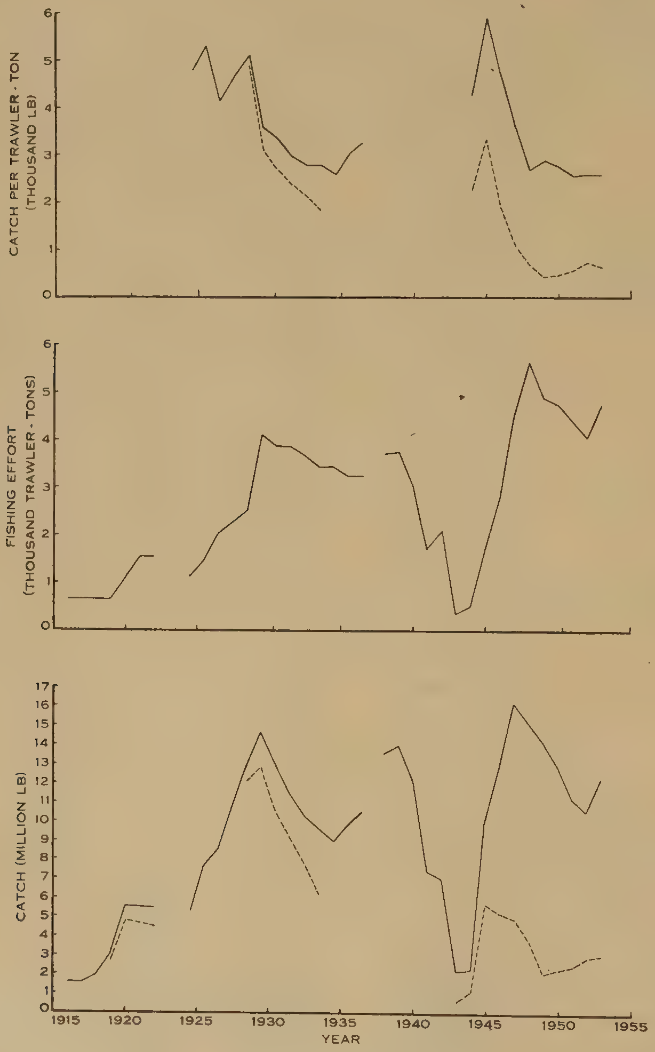

Fig. 1.—Landed catch, total fishing effort and catch per unit effort for the combined steam trawler and Danish seine fleets. Curves for catches: ——— all species; – – – tiger flathead.

The second column of Table 1 refers to catches made by steam trawlers and Danish seiners only, and these catches, with the corresponding fishing effort totals given in the third column, were used to derive the catch per unit effort values in the fourth column.

The fifth column includes, for certain years, landings from vessels not strictly in the two abovementioned categories. However, as the landings from these vessels were small and since their fishing effort could not be accounted for in a way comparable to those of the steam trawler and Danish seiner fleets, their contributions both to catch and fishing effort had to be ignored elsewhere in this paper.

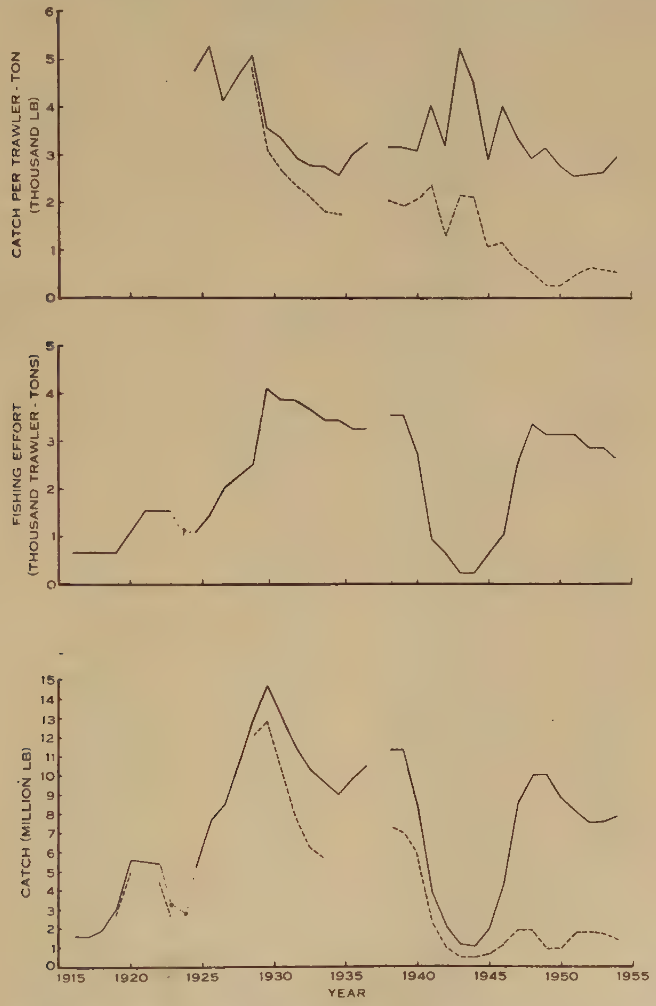

Fig. 2.—Landed catch, fishing effort, and catch per unit effort for steam trawlers only. Curves for catches: ——— all species; – – – tiger flathead.

The overall general course of the trawlfishery for all species is illustrated in Figure 1, which shows that there were three periods when fishing appears to have been relatively good in respect of both total catch and catch per unit effort. It can also be seen that these good periods were

TABLE 2

LANDED CATCH (ALL SPECIES), FISHING EFFORT, AND CATCH PER UNIT EFFORT (STEAM TRAWLERS ONLY)

Year	Catch (lb)	Number of Vessels Working	Fishing Effort (trawler-tons)	Catch per Trawler-ton (lb)
1915-16	1,630,380	3	660	
1916-17	1,637,070	3	660	
1917-18	1,897,650	3	660	
1918-19	3,023,640	3	660	
1919-20	5,585,160	4-7	1100	
1920-21	5,527,140	7	1540	
1921-22	5,404,680	7	1540	
1922-23 (8 months)	3,258,240	7	1540	
1923 (5 months)	2,867,200			
1924	5,302,155	5	1117	4747
1925	7,694,757	5-8	1455	5288
1926	8,461,600	9	2044	4139
1927	10,673,600	10	2294	4652
1928	12,785,920	11	2514	5085
1929	14,693,000	17	4103	3581
1930	12,972,827	16	3883	3341
1931	11,421,412	16	3883	2941
1932	10,285,625	15	3683	2793
1933	9,556,260	14	3443	2775
1934	8,860,740	14	3443	2573
1935	9,772,350	13	3243	3013
1936	10,539,340	13	3243	3250
1937-38	11,308,150	14	3567	3170
1938-39	11,350,850	14	3567	3182
1939-40	8,477,560	7-14	2740	3094
1940-41	3,856,580	4	949	4064
1941-42	2,119,430	3	662	3202
1942-43	1,248,670	1	237	5269
1943-44	1,076,058	1	237	4540
1944-45	1,854,304	1-4	635	2920
1945-46	4,188,673	4-5	1033	4054
1946-47	8,524,502	6-11	2515	3389
1947-48	9,986,712	11-12	3383	2952
1948-49	10,029,072	12	3157	3177
1949-50	8,797,225	11-12	3157	2786
1950-51	8,134,287	11-12	3157	2576
1951-52	7,523,042	11	2886	2607
1952-53	7,638,597	11	2886	2647
1953-54	7,807,144	10	2604	2998

preceded respectively by periods of low, reduced, and low fishing intensity. The first good period occurred around 1929, following the early developmental stage of the fishery, the second followed the years when there had been a voluntary reduction of the fleet from 17 steam trawlers in 1929 to 14 in 1934 (see Table 2), and the third occurred in the immediate post-war years, after the reduction in the fleet which had been imposed by the war.

During the years when fishing was relatively good the fishing intensity, measured in trawler-tons, was comparatively high, and it can be seen in Figure 1 that each good period was succeeded by a period of fishing that was relatively poor in respect of total catch and catch per unit effort.

To determine whether or not the changes in production from this fishery are the result of fishing or of natural fluctuations, the general picture must be dissected into its component parts. The contributions made by the two gears will be examined first.

TABLE 3

LANDED CATCH (ALL SPECIES), FISHING EFFORT, AND CATCH PER UNIT EFFORT (DANISH SEINERS ONLY)

Year	Catch (lb)	Number of Licences Issued in the Year	Estimated Av. No. of Vessels Working in each Month	Fishing Effort ("trawler-tons")*	Catch per "Trawler-ton" (lb)
1937-38		5	5	150	
1938-39		6	6	180	
1939-40		10	10	300	
1940-41		26	26	780	
1941-42		49	49	1470	
1942-43	991,392	19	4	120	
1943-44	1,199,092	60	10	300	3997
1944-45	8,215,503	97	36	1080	7606
1945-46	8,603,202	105	57	1710	5031
1946-47	7,640,600	125	67	2010	3801
1947-48	5,193,124	134	75	2250	2308
1948-49	4,123,345	110	58	1740	2369
1949-50	4,116,168	61	52	1560	2639
1950-51	3,095,877	50	41	1230	2517
1951-52	2,987,161†	51	39	1170	2553
1952-53	4,642,445†	79	63	1890	2456
1953-54					

* One Danish seiner = 30 trawler-tons.

† Excludes catches of Australian "salmon" (*Arripis trutta*). See text for explanation.

(*d*) *Total Landings from the Steam Trawlers*

The contributions made in successive years by the steam trawler fleet to the annual total landings of fish and to total fishing effort are given in Table 2 and Figure 2.

Table 2 shows that annual catches of 12 to 14 million lb of fish were landed in the years 1928-1930. From the inception of the industry to date, these figures represent "best ever" production for the steam trawlers. In the 1931-1939 period, catches ranging from 9 to 11 million lb were made and in recent years catches of 7½ to 8 million lb were more typical.

(e) *Total Landings from the Danish Seiners*

Although the Danish seine gear has been used effectively on the New South Wales coast since 1936, catch and fishing effort statistics are available only from 1942-43, and these are given in Table 3.

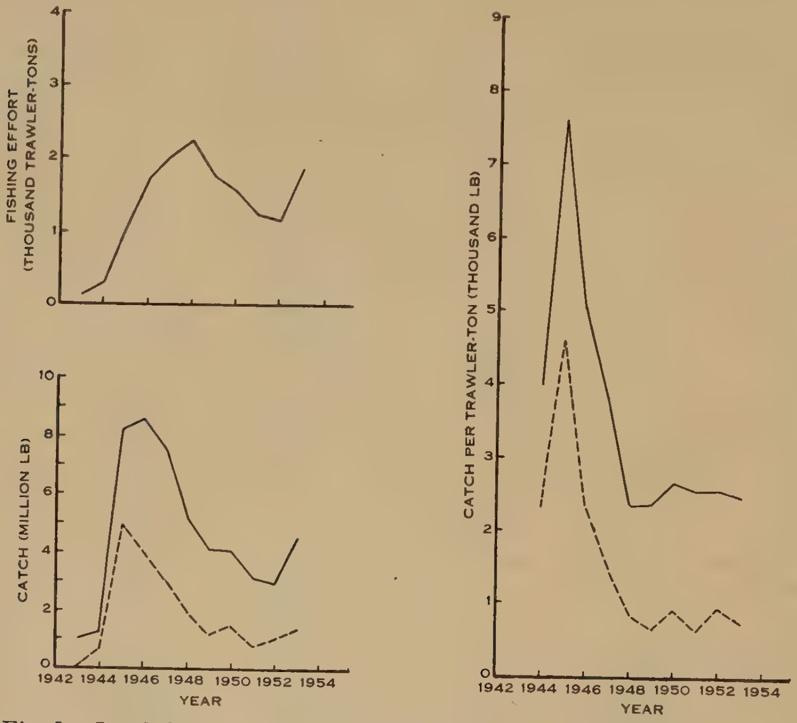

Fig. 3.—Landed catch, fishing effort, and catch per unit effort for Danish seiners only. Curves for catches: ——— all species; – – – tiger flathead.

Annual total catch from this type of gear reached a peak (8½ million lb) in 1945-46. The following year witnessed a decline, and the downward trend (see Fig. 3) extended to 1951-52, when only 3 million lb was landed.

The years 1944-45 to 1946-47 appear to have been the "best ever" years for Danish seine fishing.

Tables 1, 2, and 3 indicate that apart from the war period and the year 1945-46, the steam trawlers each year have accounted for the major share of the total catches landed by the combined fleets.

The landed catches in the early years consisted mainly of tiger flathead. However, parallel with the initial decline in landings of tiger flathead (see Fig. 2), there was a gradual introduction of other species

TABLE 4

LANDED CATCH AND CATCH PER UNIT EFFORT (TIGER FLATHEAD ONLY)

Year	Catch (lb)			Catch per Trawler-ton (lb)		
	Steam Trawlers	Danish Seiners	Combined Fleets	Steam Trawlers	Danish Seiners	Combined Fleets
1915-16						
1916-17						
1917-18						
1918-19	2,660,768*		2,660,768*			
1919-20	4,859,037*		4,859,037*			
1920-21						
1921-22	4,431,772*		4,431,772*			
1922-23 (8 months)	2,639,142*		2,639,142*			
1923 (5 months)						
1924						
1925						
1926						
1927						
1928	12,146,624*		12,146,624*	4831*		4831*
1929	12,782,910*		12,782,910*	3116*		3116*
1930	10,378,240*		10,378,240*	2673*		2673*
1931	9,137,120*		9,137,120*	2353*		2353*
1932	7,817,056*		7,817,056*	2122*		2122*
1933	6,211,530*		6,211,530*	1804*		1804*
1934	5,759,481*			1673*		
1935						
1936						
1937-38	7,350,265*			2061*		
1938-39	7,037,496*			1973*		
1939-40	5,764,700*			2104*		
1940-41	2,275,335*			2398*		
1941-42	868,954*			1312*		
1942-43	506,180	26,893	543,073	2178		
1943-44	505,785	704,163	1,209,948	2134	2347	2253
1944-45	701,634	4,960,980	5,662,614	1105	4594	3302
1945-46	1,229,343	3,988,241	5,217,584	1190	2332	1902
1946-47	1,900,940	3,074,584	4,975,524	758	1530	1099
1947-48	1,945,566	1,891,621	3,837,187	575	841	681
1948-49	930,110	1,197,152	2,127,262	295	688	434
1949-50	885,038	1,462,118	2,347,156	280	937	498
1950-51	1,707,978	817,791	2,525,769	509	665	576
1951-52	1,832,989	1,108,343	2,941,332	635	947	725
1952-53	1,736,648	1,388,947	3,125,595	602	735	654
1953-54	1,433,654			551		

* Estimates based on data given by Fairbridge (1952, Table 5).

onto the previously selective market. These other species, particularly morwong and nannygai, have figured more prominently in the total landings of recent years, and in fact less tiger flathead was landed in certain of the post-war years than either morwong or nannygai (cf. Tables 4-6).

For this reason it is appropriate to examine at this stage the individual catch and effort statistics for the three main species.

(*f*) *Catch by Species*

The annual catches and catch per unit effort data relating to tiger flathead, morwong, and nannygai for the respective gears are given in Tables 4-6 for the years for which data are available.

Tiger flathead is considered first. Except for the minor improvement just prior to the 1939-1945 war, there has been a general downward trend in catch and catch per unit effort since 1929 for the steam trawlers (see Fig. 2). The degree of decline can be judged from the following comparison. Annual total catches for the steam trawlers in the years 1932 and 1948-49 were in the region of 10 million lb. In 1932 the tiger flathead catch was approximately 76 per cent. of the total, but in 1948-49 only 10 per cent. of the total. The catch of tiger flathead per unit effort for the respective years has been calculated as 2122 lb and 295 lb per trawler ton.

TABLE 5

LANDED CATCH AND CATCH PER UNIT EFFORT (MORWONG ONLY)

Year	Catch (lb)			Catch per Trawler-ton-month* (lb)		
	Steam Trawlers	Danish Seiners	Combined Fleets	Steam Trawlers	Danish Seiners	Combined Fleets
1942-43	19,860			6		
1943-44	1,600	13,546	15,146	1	4	3
1944-45	267,369	261,760	529,129	36	20	26
1945-46	1,601,512	359,624	1,961,136	117	18	57
1946-47	3,451,753	485,711	3,937,464	132	20	78
1947-48	3,556,025	437,208	3,993,233	110	16	67
1948-49	2,559,309	489,478	3,048,787	71	23	54
1949-50	2,040,640	461,857	2,502,497	58	25	47
1950-51	1,804,834	353,304	2,158,138	51	24	45
1951-52	2,052,933	224,694	2,277,627	72	16	54
1952-53	2,570,224	538,125	3,108,349	81	24	57
1953-54	2,043,394			68		

* The method for determining this unit of fishing effort is given in Section III(*d*).

The Danish seiner catches of tiger flathead are known only for the year 1942-43 and onwards, but from material already presented in Tables 1 and 3 it can be seen that the greatest annual catch (5 million lb), was landed in the year 1944-45. The general trend of catch and catch per unit effort has been downward, however, since that year (see Fig. 3).

The data concerning tiger flathead catch for the combined fleets are somewhat sketchy, owing to a lack of information for the Danish seiners, but may be supplemented by reference to Figure 1 in conjunction with Figure 2.

TABLE 6

LANDED CATCH AND CATCH PER UNIT EFFORT (NANNYGAI ONLY)

Year	Catch (lb)			Catch per Trawler-Ton-Month* (lb)		
	Steam Trawlers	Danish Seiners	Combined Fleets	Steam Trawlers	Danish Seiners	Combined Fleets
1942-43	132,880			40		
1943-44	54,233	139	54,372	25		9
1944-45	82,601	24,100	106,701	11	2	5
1945-46	751,685	53,495	805,180	55	3	24
1946-47	1,846,977	133,960	1,980,937	71	6	39
1947-48	3,250,655	240,070	3,490,725	101	9	59
1948-49	4,976,564	481,163	5,457,727	139	23	96
1949-50	4,556,926	330,692	4,887,618	130	18	92
1950-51	2,105,272	686,371	2,791,643	60	47	58
1951-52	825,803	91,616	917,419	29	7	22
1952-53	1,085,710	451,704	1,537,414	34	20	28
1953-54	1,586,626			52		

* See footnote to Table 5.

The catches of morwong and nannygai landed by the Danish seiners are only a small portion of the total and need not be considered here.

The features to be noted about the landings of morwong and nannygai from steam trawlers are as follows: the best years (catch per unit effort) were 1945-46 to 1947-48 for morwong and 1947-48 to 1949-50 for nannygai, and following these peaks of availability there have been sharp declines to comparatively low levels.

(*g*) *Summary*

A brief summary dealing with the main peaks in production is given here.

The course of the fishery, up to the time of the first peak in production, is what would be expected as typical of the initial development of a trawlfishery.

The second peak can be explained partly as the result of three changes: the gradual introduction of other species on to the market, the introduction of a new gear, the Danish seine, and improved landings of tiger flathead from the steam trawlers.

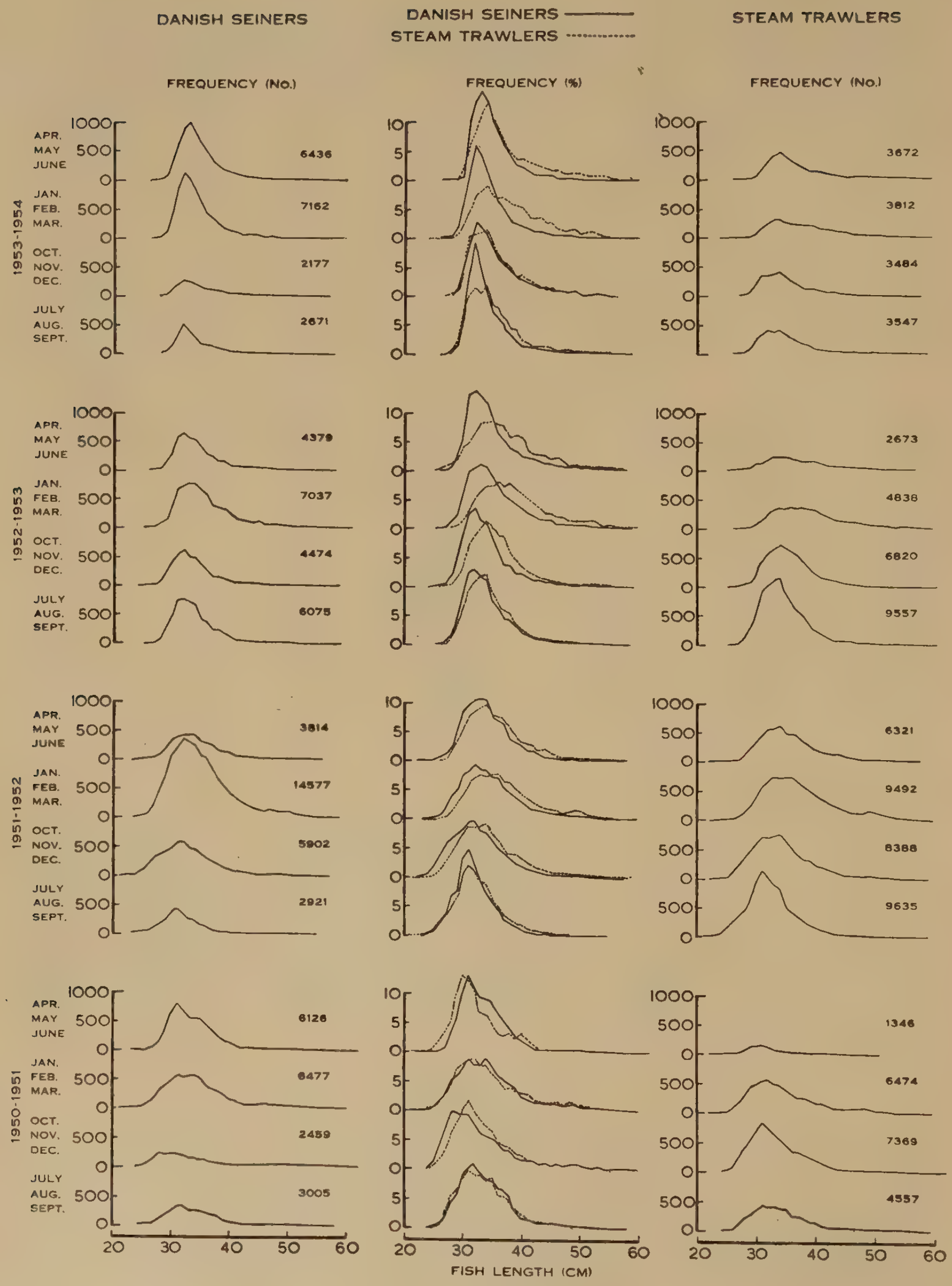

Fig. 4(*a*).—Comparison of the quarterly length frequency and percentage length frequency polygons (1-cm groupings, mean length recordings), derived from samples of tiger flathead measured in the Sydney Fish Market. Numbers of fish measured are given for each quarter. Years 1950-51 to 1953-54.

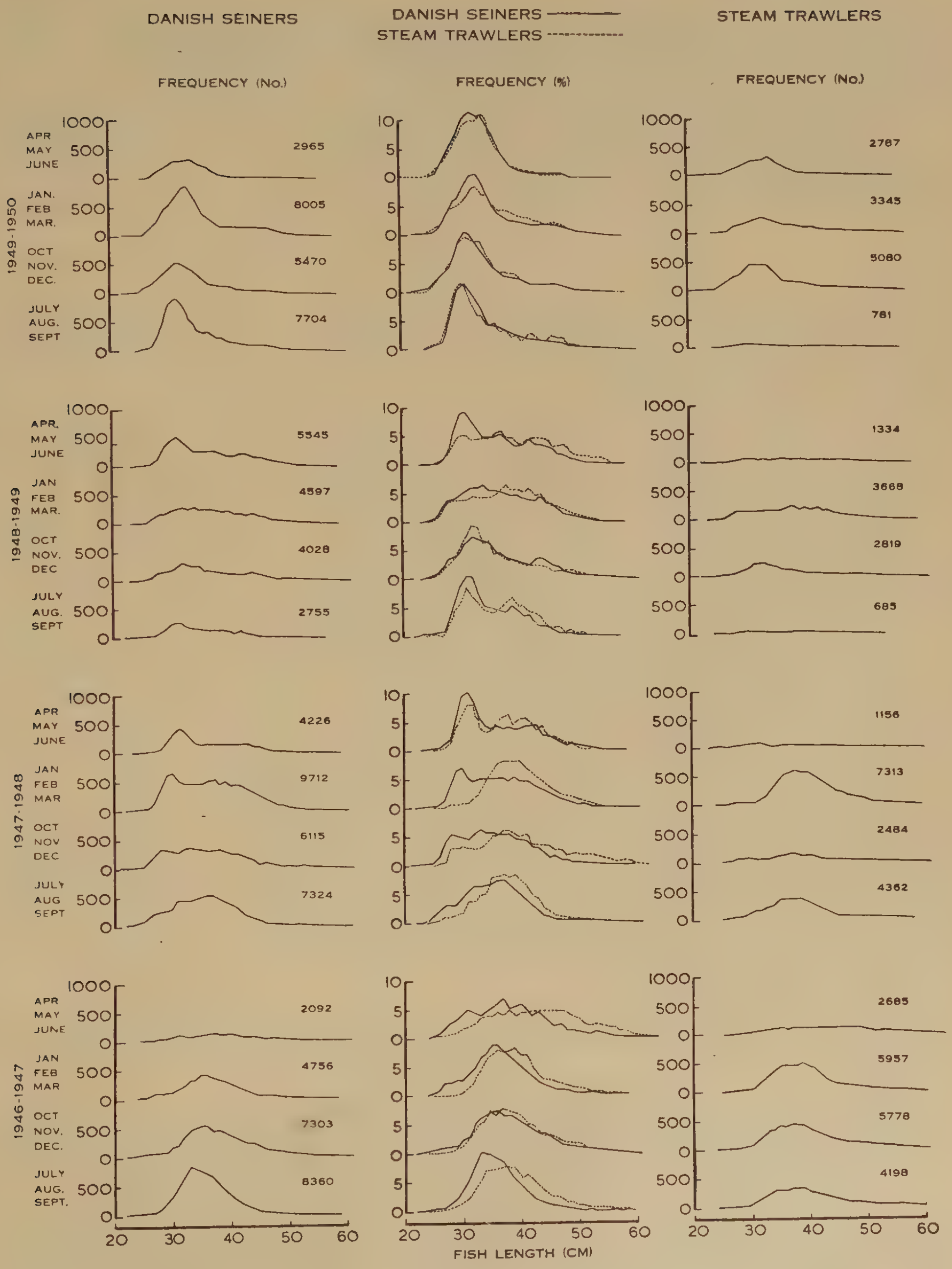

Fig. 4(*b*).—Comparison of the quarterly length frequency and percentage length frequency polygons (1-cm groupings, mean length recordings), derived from samples of tiger flathead measured in the Sydney Fish Market. Numbers of fish measured are given for each quarter. Years 1946-47 to 1949-50.

The rise to the third peak of production, and the maintaining of it for a few years, can be attributed in the main to the following successful landings: tiger flathead from Danish seiners, morwong from steam trawlers, and nannygai from steam trawlers, in that order of appearance.

Further discussion centring on these peaks in production is given later. It is now appropriate to endeavour to account for the downward trends of catch and catch per unit effort.

III. THE FISHERY FOR TIGER FLATHEAD

(*a*) *General*

In Section II attention was drawn to the very marked reductions in the landed catch of tiger flathead and the catch per unit effort for that species, and particularly the reductions which occurred in the post-war years. As tiger flathead was the most important and abundant species during the early years of the fishery an examination of the past changes in availability of this species should indicate the remedial measures to be taken to improve the present depleted condition of this fishery. Such an examination should include a consideration of year to year changes within the fish stock itself. Limited information, however, is available on this latter subject, and this only for recent years.

The lack of data has necessitated a less direct approach to an analysis of the past course of the tiger flathead fishery. The effects of recent changes in the size and age compositions of the landed catches and the probable causes for these changes will be considered first, and the results then used in an attempt to explain the past changes in production.

Three important conclusions reached by Fairbridge (1951) were taken into account when the data treated in the following Sections, III(*b*) and III(*c*), were drawn up for consideration. These were: firstly, that the presence of distinct populations of tiger flathead in New South Wales waters can be discounted for all practical purposes; and secondly and thirdly, that the differences in growth rate between sexes, and between localities, are only small.

(*b*) *Size Composition of the Landed Catch of Tiger Flathead in Recent Years*

The data treated in this section were collected in the Sydney Fish Market, where most of the marketable catches of tiger flathead landed in New South Wales are handled for sale.

Under the direction of the late Mr. W. S. Fairbridge, a full sampling programme was designed to provide a yearly estimate of the age composition of the landed commercial catch. The programme (see Fairbridge 1951, 1952) commenced in July 1946, and with slight modifications was modelled on the method described for herring by Hodgson (1939).

Part of the sampling procedure has been to measure a representative sample of tiger flathead passing through the market each day, in this way endeavouring to make approximately 4000 random measurements each month. The programme has been carried out throughout by the same person and although it was not always possible to achieve the total aimed at, the degree of success can be judged from the quarterly totals given to the right of the length frequency polygons in Figures 4(*a*) and 4(*b*).

All flathead measurements are for total length (cm). They are mean length recordings; e.g. fish from 32.5 to 33.4 cm are recorded as 33 cm.

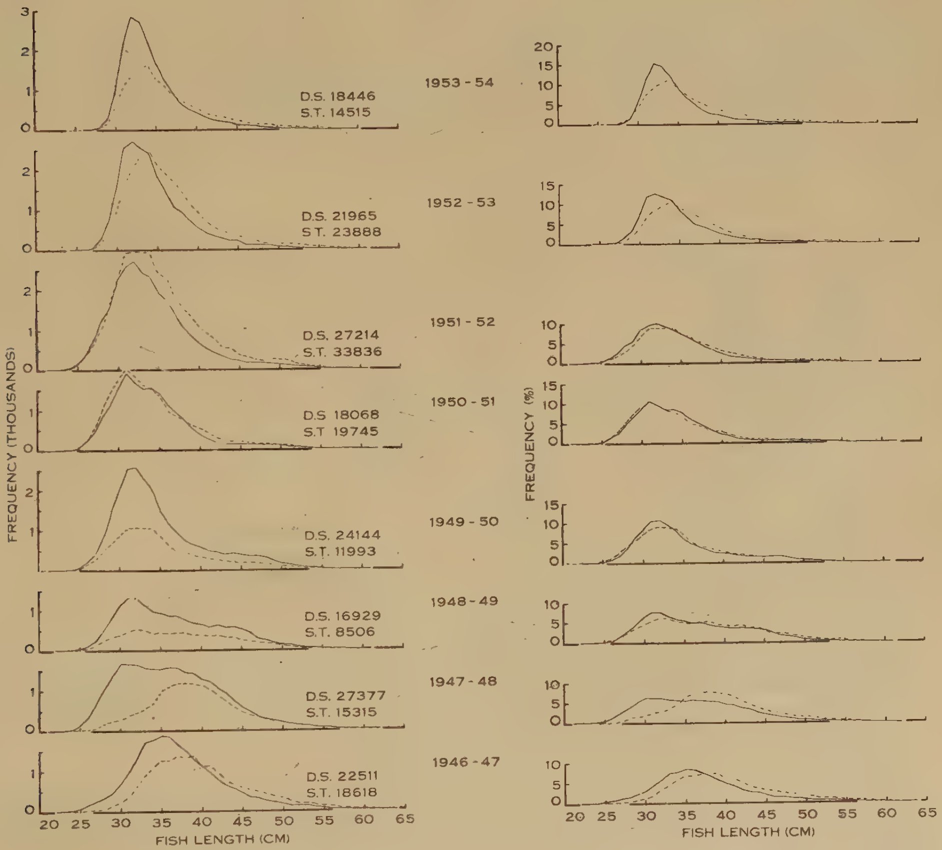

Fig. 5.—Comparison of the annual length frequency and percentage length frequency polygons (1-cm groupings, mean length recordings) derived from samples of tiger flathead measured in the Sydney Fish Market. Actual numbers measured are given for each year. ——— Danish seiners; – – – steam trawlers.

Annual length frequency distributions (1-cm groupings) were compiled from the monthly measurements, and the length frequency and percentage length frequency polygons shown in Figure 5 were drawn up from these distributions. The data from Danish seiners and steam trawlers respectively were treated separately for the purpose of comparison.

The comparison reveals that except in the years 1946-47 and 1947-48 the length frequency distributions for the samples from the two types of gear are essentially similar in any year.

The reasons for the small differences between the length frequency distributions for the two gears in any one quarter or year are not known with certainty. They can be tentatively accounted for, however, in the following ways: firstly, the Danish seiners rarely fish at night, whereas the steam trawlers do, and if the habits of the fish are different during the day and at night this could give rise to variations in catch; secondly, the fish possibly react quite differently to the two types of gear both before and after capture, that is, at the time when the gears are working on the bottom; and thirdly, it is probable that some grounds are suitable for one type of gear and not the other (e.g. the otter-trawl gear can be operated in deeper water than the seining gear).

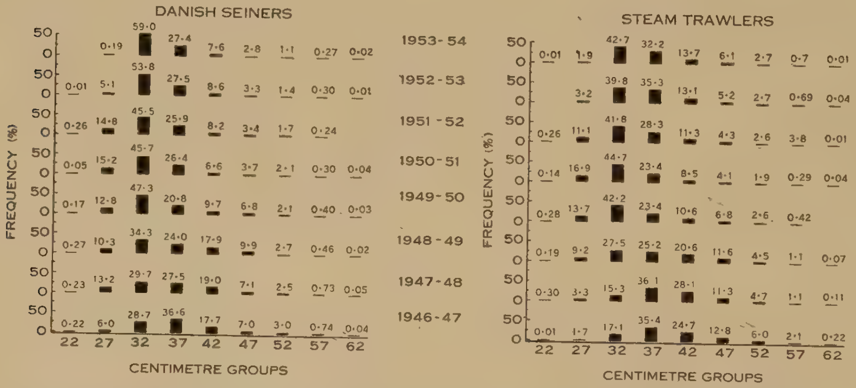

Fig. 6.—Comparison of the annual percentage length frequency histograms (5-cm groupings, mean length recordings), derived from the flathead length measurements taken in the Sydney Fish Market. Values above each class interval are actual percentages of the total measured in each year.

However, as the comparative efficiency of the two gears has not been tested in these waters, and since at present it is not possible to determine locality, depth, or time of capture for any of the samples taken in the Sydney Fish Market, it would serve little purpose to carry this reasoning further. The problem must be left in abeyance until sea-going facilities are made available on either commercial vessels or a research vessel.

The relatively steep, truncated, left-hand arms of the length frequency polygons for 1952-53 and 1953-54 in Figure 5 reflect, not the availability on the fishing grounds of tiger flathead of the lower size groups as do the progressively steepening right-hand arms for the higher size groups, but a change in marketing control, which resulted in a more rigid interpretation of the regulation concerning legal length by the fishermen when sorting fish to be sent to the market.

This sampling for size composition of the commercial landed catch shows how the emphasis of the fishery has changed since 1946-47, presumably owing to a scarcity of fish of the higher size groups, and shows that at present the fishery is dependent on fish ranging around a modal length of 33 cm. This length corresponds to the existing minimum legal length for tiger flathead in New South Wales. The percentage of undersized fish passing through the Sydney Fish Market is indicated, therefore, by the percentage length frequency polygons in Figure 5 and by the percentages given above the class intervals in the length frequency histograms of Figure 6.

The falling off of fish size since 1946-47, equally for both types of gear, is demonstrated clearly in Figure 6.

(*c*) *Age Composition of the Landed Catch of Tiger Flathead in Recent Years*

The first attempts to use otoliths from tiger flathead for age determinations were made in the Department of Zoology, University of Sydney, under the direction of the late Professor W. J. Dakin. A description of the otoliths with an account of the presence of periodic rings of growth, displaying a regular seasonal rhythm, which could be used for an estimation of age in this species, is presented by Dakin (1939). Fairbridge (1951, 1952) describes the methods of collecting and reading the otoliths.

The raw data for calculating the annual age composition of the landed catches of tiger flathead consisted of the following material. The monthly random length measurements referred to in Section III (*b*) were considered to be representative samples of the tiger flathead landed catches. A separate subsample (25 fish each week, chosen as far as possible to cover the length range of fish entering the market), provided details of whole and gutted weights, sex proportions, gonad stages, and gonad weights, with corresponding length measurements. Otoliths were removed from these fish and stored dry in their respective pence envelopes. Further random samples of otoliths were collected along with the corresponding fish lengths, bringing the total number of otoliths collected to approximately 100 each week, i.e. 50 from flathead caught by steam trawlers and 50 from those caught by Danish seiners.

As mentioned earlier, the full sampling programme commenced in July 1946, but few otoliths were collected from early 1950 to September 1952, and consequently it was not possible to make age composition estimates for the years 1949-50 to 1951-52.

To obtain estimates of the age compositions for 1952-53 and 1953-54, the raw data were treated for each type of gear separately, as follows:

(i) Length frequency distributions were compiled for each quarter from the random measurements collected in the market.

(ii) Otoliths were read for age and quarterly length-age distribution tables were drawn up.*

(iii) A third table was compiled for each quarter, in which the frequencies at each 1-cm group in the length frequency table (i) were dissected into age groups from the proportions set out in the length-age table (ii).

(iv) The frequencies in each age group were then multiplied by the corresponding estimated mean whole weight (oz) of each 1-cm group.† The products so derived were summed for each age group, giving a weight value (*d*), and the sum of these age-group weights gave an estimated total weight (*b*) for the quarterly sample.

(v) The actual weight of tiger flathead taken by the particular type of gear in the quarter was converted to ounces (*a*).‡ This quantity (*a*) was divided by the estimated weight of the quarterly sample (*b*) to give a factor (*c*).

(vi) The calculated weights of each age group (*d*) were multiplied separately by the factor (*c*), thus giving the estimated weights (*e*) of tiger flathead of each age group, caught by the particular gear in the quarter.

(vii) The estimated number of flathead of each age group was obtained by dividing each value of (*e*) by the average weight of the appropriate age group, which was calculated from the material in table (iv).

(viii) Yearly totals for each gear and grand totals for the combined fleets were subsequently determined from the quarterly results.

The estimated numbers of fish of each age-group landed by the combined fleets during the years 1952-53 and 1953-54 are given in Table 7, together with similar unpublished results obtained by the late Mr. W. S. Fairbridge for the period 1946-47 to 1948-49. The latter results were used in constructing the age composition histograms of Fairbridge (1952, Fig. 1).§

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* There were insufficient otoliths for the quarter July-September 1952 for Danish seiners and steam trawlers, and for the quarter October-December 1952 for Danish seiners. The corresponding quarterly length-age distribution tables for 1953 were used therefore to derive tables (see (iii) below) in each case.

† Fairbridge (1952, pp. 4 and 5) describes the method of estimating the mean whole weight at each 1-cm group, from the subsample material.

‡ When these calculations were made the Danish seine catch figure for the quarter April-June 1954 had not been finalized. The known catch for the quarter was given as 129,762 lb. From general experience of the seasonal landings recorded for previous years, 100,000 lb was added to the above value to give an estimated total for the quarter. This is considered to be a generous estimate of the final published catch in the New South Wales Fisheries Branch's Annual Report for 1953-54.

§ The side legend to Figure 1 in Fairbridge (1952, p. 6) should read "Numbers (100,000's)" and not "Numbers (millions)" as shown.

TABLE 7

NUMBERS OF FLATHEAD OF EACH AGE GROUP LANDED BY THE COMBINED FLEETS

Year	Number in Age Group (× 1000)							Total Trawler-tons	Total Trawler-ton-months*	Av. No. of Danish Seiners Working	No. of Steam Trawlers Working	Catch (lb)
	II+	III+	IV+	V+	VI+	VII+	VIII+					
1946-47	5	593	2007	1633	550	117	21	4525	50,247	67	6-11	4,975,524
1947-48	7	732	977	1584	545	101	18	5633	59,301	75	11-12	3,754,046
1948-49	2	438	892	564	142	39	5	4897	56,761	58	12	1,852,155
1949-50/51-52				Not known								
1952-53	66	570	1383	1112	332	98	18	4776	54,550	63	11	3,125,595
1953-54	50	653	1108	767	229	71	19	4704†	55,832†	70†	10	2,348,318†

* See text for explanation.

† Includes estimations for the quarter April to June 1954, for Danish seiners. See third footnote, p. 184, for explanation.

The catch values given in Table 7 were those used in calculating the numbers of fish in each age group.

It will be noted that the catch totals in Table 7 for 1947-48 and 1948-49 (Fairbridge, unpublished data) are at variance with those presented earlier in Table 4, which were extracted from the Annual Reports of the New South Wales Fisheries Branch. After examining the late Mr. W. S. Fairbridge's unpublished material the author was unable to account for the 1947-48 difference but since the difference is only small, it can be reasonably discounted. The conflicting figures for 1948-49 were found to result from the omission of one month's landings.

Before incorporating the results from the earlier years with those for 1952-53 and 1953-54, it was necessary to determine whether the methods of interpreting otoliths for age used by the late Mr. W. S. Fairbridge and the author were strictly comparable.

In Table 8 are given the total length-for-age readings, determined from the 1952-53 and 1953-54 otolith material by the author, and similar data for earlier material by Fairbridge (1951, pp. 163-4, Table 8).

It will be seen from Table 8 (this paper) that there is a uniform difference between the two sets of data, a difference which can be eliminated either by transferring the left-hand groups of values in each age group column to the age group columns next below or the right-hand ones to the age group columns next above. This comparison of results suggested that the age interpretations made by the late Mr. W. S. Fairbridge and the present author differed by 1 year in each case.

A difference of 1 year in age readings was revealed also when a comparison was made of the quarterly age-length distribution tables, "weighted" by their respective quarterly length frequency distributions (for method see Section III(*c*)(iii)).

Figure 7 illustrates the results obtained by treating certain of the material from both periods in this manner. The length frequency distributions for the particular quarters are represented by the percentage length frequency polygons.

The age-group polygons of Figure 7 show that the main mode and the length spread of an age group from the earlier material (Fairbridge, unpublished data) correspond closely with similar characteristics for the next higher age group in the later material (the author's).

There were two alternatives to be considered in view of the differences outlined above:

(i) The age readings as originally determined by the two workers were both valid and the results obtained strictly comparable;

(ii) One or the other set of age readings was incorrect as the result of misinterpretation of the otolith pattern (the difference amounting to 1 year in each determination, the present author's readings being the higher), in which case an adjustment to one set of results would be

TABLE 8

AGE DETERMINATIONS OF FLATHEAD

Numbers given on the left-hand side of each age-group column derived from 1952-53 and 1953-54 otolith readings by the author, those on the right-hand side from Fairbridge (1951, Table 8), from earlier material

Total Length Groups (cm)	Number in Age Group											
	0+	I+	II+		III+		IV+		V+	VI+	VII+	VIII+
5		2										
6		3										
7		—										
8		5										
9		24										
10	1	25										
11	1	23										
12	1	20										
13		23										
14		23										
15		31										
16	1	28										
17		42		1								
18	1	18		1								
19		4		1								
20		14		3								
21		15		10								
22		40		15								
23		50		41								
24		41		75								
25		25		150								
26		18	1	136		3						
27		8	2	206	2	8						
28		13	8	172	8	13	1					
29		6	15	164	31	35	5					
30		2	9	109	105	41	31	1				

TABLE 8 (*Continued*)

Total Length Groups (cm)	Number in Age Group														
	0+	I+	II+		III+		IV+		V+		VI+		VII+		VIII+
31			7	88	184	97	124	1	7						
32			3	70	167	141	245	5	14						
33			3	31	141	193	355	10	50						
34				20	66	164	349	33	118						
35				10	31	194	262	69	157		4				
36				2	17	177	189	101	193		11				
37				4	5	134	159	159	194	1	21		1		
38				3	6	123	108	189	203	5	30		1		
39				2	1	92	75	195	169	8	31		1		
40				2		79	52	201	174	17	48		10		
41						41	32	173	139	33	50	1	5		
42						25	20	183	108	29	52	—	9		
43						18	11	118	88	43	59	2	10		
44						8	7	98	60	44	64	2	4		
45						5	2	98	49	42	75	1	11		
46						3		66	29	51	79	1	11		
47								54	18	74	43	2	7		
48								35	12	46	33	5	5		2
49								18	2	52	33	10	7		2
50								15	3	50	28	3	11		2
51								8	2	39	21	8	5		9
52								2		33	16	10	10		12
53								2		34	6	9	7		13
54										17	2	17	10	1	7
55								1		4		20	1	1	5
56										7	1	7	1	3	8
57										—	1	7	1	1	2
58										2		8		2	3
59										1		5		1	2
60												1	1	—	2
61												1		—	
62														1	1

necessary before comparing the age composition material for the respective years.

Alternative (i) was discounted on the grounds that if accepted, there were two anomalies for which there were no adequate explanations. The first was that the results would have shown a decreased length for age, a condition more likely to arise in densely populated stock; and evidence already presented (a very marked decline in catch and catch per unit effort) suggests that this condition is unlikely for the tiger flathead stock. The second anomaly was that the age composition estimates would have shown yearly changes incompatible with those revealed by the length frequency polygons in Figure 5. The measure of inconsistency can be gauged by reference to Figure 8; if the histograms of the three earlier years were moved one age-group interval to the left (i.e. left as originally determined by Fairbridge (1952, p. 6, Fig. 1)), then the age composition estimates would show that more fish of the higher age groups, and less of the lower, were landed in 1953-54 than in 1946-47. This is quite contrary to what would be expected if the length frequency polygons of Figure 5

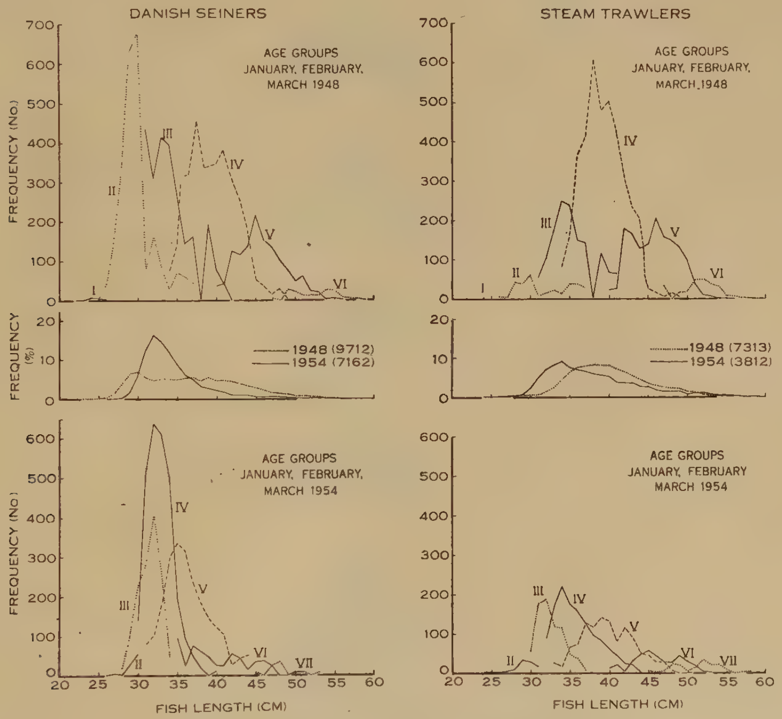

Fig. 7.—Comparison of selected quarterly age-length distribution tables "weighted" by the corresponding quarterly length frequency distributions. (Numbers in brackets refer to numbers of flathead measured for length in the particular quarter.)

are taken as a guide to the real nature of the changes in age composition of the landed catches.

Since the acceptance of alternative (i) would thus have given irrational results, and as the author has reason to believe that the age of the earlier material was underestimated by 1 year,* the necessary adjustment was made for the earlier misinterpretation. The addition adjustment has already been applied to all tabular and graphical data on the age composition of the commercial landed catches in this paper, and no further adjustment is necessary.

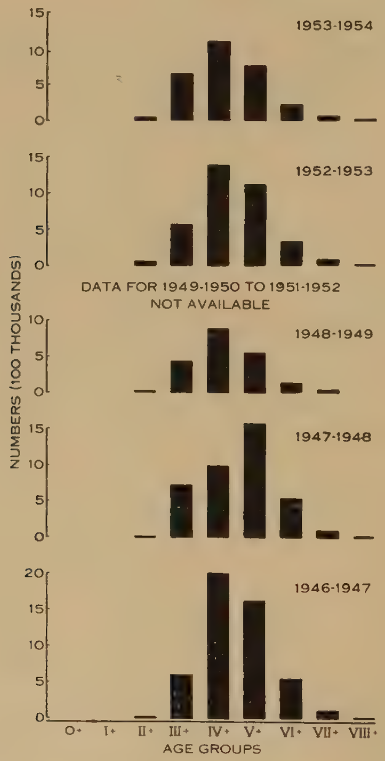

Fig. 8.—Age composition (estimated numbers of fish of each age group) of the landed catch of tiger flathead for certain years, for all vessels.

(d) *Examination of the Recent Changes in the Age Composition*

The changes in age composition of the landed catches from the combined fleets (see Fig. 8), can be interpreted only by examining the separate results for the two fishing gears.

Set out in Table 9, Table 10, and diagrammatically in Figure 9, are the quarterly and annual estimated numbers of fish of each age group landed from the steam trawlers and Danish seiners in certain years. Owing to the method of treatment of some of the earlier data by Fairbridge it was not possible to include comparable results for the years 1947-48 and 1948-49. Alongside the estimates for each quarter are given the catch (lb), and the fishing effort required for this catch. It was pointed out in Section II (*b*) that the fishing effort can be defined only by an insensitive measure. Some slight refinement is possible, however, by using the trawler-ton-month (see Fairbridge 1948) as the unit of fishing effort; this is obtained for steam trawlers by summing the products of gross tonnage and the number of months each vessel was working, and for Danish seiners by multiplying the average number of vessels working during the year by 30, to give trawler-tons, and the resulting product by 12, to give "trawler-ton-months".

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* A later paper, dealing with the interpretation of the otolith pattern as a means of estimating the age of tiger flathead, will include discussion to support this belief.

Both measures of fishing intensity (i.e., trawler-tons and trawler-ton-months) are unsuitable for calculating the rate of catch of fish of the individual age groups, but the results as presented do enable the relative availability of fish of the IV+ and higher age groups to be indirectly compared in the years for which information is available.

It will be seen from Table 9 that despite the increased fishing effort in the two later years, fewer fish of the V+ to VIII+ age groups were landed by the steam trawlers than in the year 1946-47. However, there was an increase in landings of the IV+ age-group fish, and a very marked increase in the numbers of the II+ and III+ age groups. A point worth noting from these estimations for steam trawlers is that fewer fish were landed in 1946-47 than in either of the other two years, and yet a greater weight of fish was landed in the earlier year, when less fishing effort was expended. This is one of the effects of the falling off of fish size mentioned in Section III (*b*).

For the Danish seiners the pattern of change has been somewhat different. Table 10 shows that apart from fish of the II+ age group there has been an overall reduction in the numbers of fish of all age groups landed by this gear, and that there was a considerable decline in catch (lb) for the Danish seiners even though the fishing effort was practically the same in the three years. The drop in numbers of the V+ to VIII+ age-group fish closely parallels the reduction noted in the same age groups for steam trawlers.

(*e*) *Probable Causes for the Recent Changes in Size and Age Composition*

It will be appreciated that owing to the small amount of data available it is not possible to give a precise analysis of the causes for the recent changes in age composition of the landed catches in successive years since 1946-47. However, as there would seem to be an urgent necessity for a solution to the deteriorating condition of the fishery for tiger flathead (i.e. for arresting the marked decline in catch and catch per unit effort)

TABLE 9

NUMBERS OF FLATHEAD OF EACH AGE GROUP LANDED EACH QUARTER FROM STEAM TRAWLERS

Quarter	Number in Age Group (× 1000)							Total Trawler-tons	Total Trawler-ton-months	Number of Steam Trawlers Working	Catch (lb)
	II+	III+	IV+	V+	VI+	VII+	VIII+				
1946-47											
July-Sept.		11	110	180	50	7	2		5,243	6-7	365,767
Oct.-Dec.		39	227	174	59	14	5		6,505	8-9	604,771
Jan.-Mar.	0.1	16	104	175	97	17	3		6,943	9	448,939
Apr.-June	0.8	32	87	117	48	21	2		7,436	9-11	481,463
Total	1.0	97	528	646	254	59	13	2515	26,127	6-11	1,900,940
1952-53											
July-Sept.	13	174	219	79	14	6	6		7,845	10	380,020
Oct.-Dec.	14	70	167	116	28	10	4		7,597	9-10	349,622
Jan.-Mar.		77	278	192	67	30	3		8,214	10-11	748,713
Apr.-June		33	100	95	32	7	0.4		8,214	10-11	258,293
Total	26	354	763	481	142	53	13	2886	31,870	9-11	1,736,648
1953-54											
July-Sept.	11	165	224	69	17				7,892	10	361,989
Oct.-Dec.	17	101	179	117	32	10	2		7,338	9-10	380,987
Jan.-Mar.	9	74	123	111	36	17	3		7,590	9-10	384,034
Apr.-June	2	49	117	109	32	16	6		7,812	10	306,644
Total	39	389	643	405	117	44	11	2604	30,632	9-10	1,433,654

TABLE 10

NUMBERS OF FLATHEAD OF EACH AGE GROUP LANDED EACH QUARTER FROM DANISH SEINERS

Quarter	Number in Age Group (× 1000)							Total "Trawler-tons"	Total "Trawler-ton-months"	Av. No. of Danish Seiners Working	Catch (lb)
	II+	III+	IV+	V+	VI+	VII+	VIII+				
1946-47											
July-Sept.		57	413	306	51	7	1			73	662,871
Oct.-Dec.		107	393	245	77	17	2			68	892,015
Jan.-Mar.	1	223	524	343	141	27	4			71	1,078,244
Apr.-June	3	109	149	94	27	7	1			54	441,454
Total	4	496	1479	987	296	58	9	2010	24,120	67	3,074,584
1952-53											
July-Sept.	28	78	99	73	20	8	3			56	220,133
Oct.-Dec.	5	57	101	66	14	7	3			54	180,650
Jan.-Mar.	7	70	306	272	106	16	8			70	676,829
Apr.-June		10	113	220	50	12	0.8			70	311,335
Total	40	216	619	631	191	45	15	1890	22,680	63	1,388,947
1953-54											
July-Sept.	4	94	89	59	16	5				64	181,175
Oct.-Dec.		35	61	41	19	5				77	133,283
Jan.-Mar.	7	95	199	158	39	7	4			77	370,444
Apr.-June		40	116	103	39	10	4			64*	229,762*
Total	11	264	465	362	112	28	8	2100*	25,200*	70*	914,664*

* Includes estimations for the quarter April to June 1954, for Danish seiners. See third footnote, p. 184, for explanation.

the following analysis is presented with a view to determining the probable reasons for the recent course of the tiger flathead fishery.

Table 11 gives, for the years for which information is available, statistics on fishing effort (trawler-ton-months) and catch per unit effort relating to tiger flathead. The superior catch per unit effort recorded for Danish seiners in 1946-47 (steam trawlers 73 lb/T.T.M.* and Danish seiners 127 lb/T.T.M.) can be attributed in the main to the larger numbers of the III+ and IV+ age-group fish landed by the Danish seiners in that year (cf. Tables 9 and 10). The differences between the relative proportions of the age groups for the two gears in 1946-47 can be seen in Figure 9 (see also Figs. 5 and 6, which illustrate the dissimilarity of the length frequency distributions for the two gears in that year).

TABLE 11

FISHING EFFORT AND CATCH PER TRAWLER-TON-MONTH (TIGER FLATHEAD ONLY)

Year	Fishing Effort (trawler-ton-months)			Catch per Trawler-ton-month (lb)		
	Steam Trawlers	Danish Seiners	Combined Fleet	Steam Trawlers	Danish Seiners	Combined Fleet
1928				367*		367*
1929				295*		295*
1930	43,146		43,146	241		241
1931	40,668		40,668	225		225
1932	38,745		38,745	202		202
1933	36,194		36,194	172		172
1934	34,753		34,753			
1935	34,750		34,750			
1936	36,092		36,092			
1937-38	41,738	1,800		176		
1938-39	41,467	2,160		170		
1939-40	28,434	3,600		203		
1940-41	10,527	9,360		216		
1941-42	7,317	17,640		119		
1942-43	3,290	1,440	4,730	157		
1943-44	2,133	3,600	5,733	237	196	211
1944-45	7,393	12,960	20,353	95	383	299
1945-46	13,734	20,520	34,254	90	194	152
1946-47	26,127	24,120	50,247	73	127	99
1947-48	32,301	27,000	59,301	60	70	65
1948-49	35,881	20,880	56,761	26	57	37
1949-50	35,007	18,720	53,727	25	78	39
1950-51	35,124	14,760	49,884	49	55	52
1951-52	28,448	14,040	42,488	64	79	69
1952-53	31,870	22,680	54,550	54	61	57
1953-54	30,632			47		

* Approximations taken from Fairbridge (1952, Table 5).

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* Trawler-ton-month.

In contrast to the differences of 1946-47, the catches per unit effort and the relative proportions of the age groups in 1952-53 were similar for the two gears (see Table 11 and Fig. 9). The relative proportions of the age groups in 1953-54 for the steam trawlers closely resembled those in the previous year for the same gear, but the catch per unit effort had dropped to 47 lb/T.T.M., compared with 54 lb/T.T.M. in 1952-53.

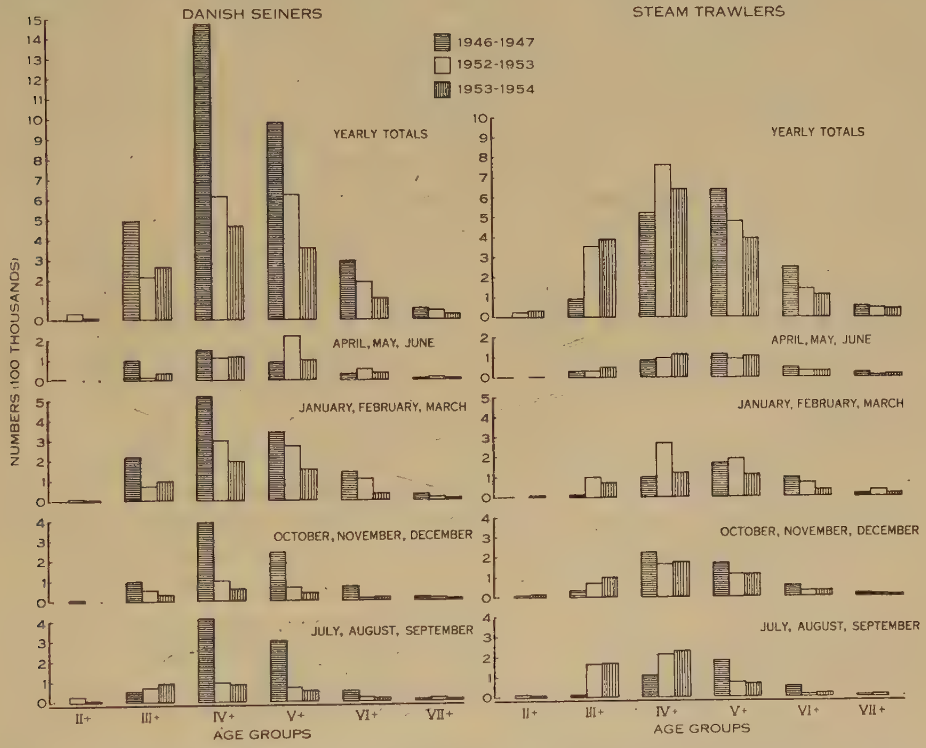

Fig. 9.—Age group histograms showing estimated numbers of flathead of each age group landed by the separate gears in certain years. Comparison of the relative proportions of the age groups of the landed catches in those years and seasonal abundance.

So far it is reasonable to assume from the landings made by the two fleets that since 1946-47 there has been a decline in the availability and hence in the density of marketable fish of the V+ to VIII+ age groups; and judging from the landings of the IV+ age-group fish made by the Danish seiners in the years 1946-47 and 1952-53, there has been a decline also in the availability and density of fish of this age group (see Table 7). It may be validly assumed from these reductions in availability of the various age-groups that the size of the population has decreased since 1946-47.

It will be seen from Figures 5 and 6 that the length frequency distributions for steam-trawled fish in the years 1952-53 and 1953-54 were similar and it has already been noted that the relative proportions of the age groups in those years were similar. It is suggested, therefore, that since there was only a minor difference between the length frequency distributions for steam-trawled fish in the years 1946-47 and 1947-48, the relative proportions of the age groups were similar in those years. Table 11 shows that the catch per unit effort for steam trawlers in 1946-47 was 73 lb/T.T.M., and in 1947-48 60 lb/T.T.M. This decline suggests a reduction in the availability (= density) of what were considered at that time to be marketable fish, for the steam trawlers.

The 1948-49 length frequency polygons (see Figs. 5 and 6) indicate a marked shortage of fish of the 35-40 cm size groups (cf. the modes for the previous two years), and even though the steam trawlers had resorted to landing fish of the smaller size groups in 1948-49 (see Fig. 5, mode at 32 cm for steam trawlers) their catch per unit effort fell sharply to 26 lb/T.T.M. (see Table 11). A probable explanation for the scarcity of fish of the higher size groups is that in the previous year the Danish seiners had landed fish of the lower size groups (see mode at 31 cm for 1947-48, Fig. 5), and it is not unreasonable to assume that the consequent increased fishing mortality of the smaller fish in 1947-48 was partly the cause of the shortage of fish of higher size groups in the following year.

By 1949-50 the reduced availability of the higher size groups was even more pronounced than in 1948-49 (see Fig. 5). This may have been partly caused by the higher fishing mortality of the lower size groups in 1948-49, since the steam trawlers also were landing smaller fish in that year.

The catch per unit effort for steam trawlers in 1949-50 was only 25 lb/T.T.M., and it would seem therefore that to maintain their catch per unit effort as high as in 1948-49 (26 lb/T.T.M.) they must have resorted to landing even more of the smaller fish than in the previous year. The catch per unit effort for the Danish seiners had improved, however, from 57 lb/T.T.M. in 1948-49 to 78 lb/T.T.M. in 1949-50, and here again they must have drawn heavily on the smaller size groups, because as already mentioned there was a marked paucity of large fish in 1949-50.

From 1950-51 the variations in catch per unit effort for steam trawlers are similar to those for Danish seiners (see Fig. 10). This is not unexpected, because from 1950-51 to 1951-52 the length frequency distributions for the two gears correspond very closely (see Fig. 5) and there is not a great deal of difference between the relative proportions of the age groups for the two gears in 1952-53 and 1953-54 (see Fig. 9).

The catch per unit effort for steam trawlers in 1947-48 was less than in 1946-47; and it was presumed earlier that as they had relied on the same age groups, which were in the same relative proportions as the previous year (this was inferred from the length frequency distributions for the two years, which showed a close resemblance), the decline in catch per unit effort was the result of reduction in the density of what was then considered to be marketable fish for the steam trawlers.

The Danish seiners in 1947-48 had resorted to landing smaller fish than the steam trawlers, and even smaller fish than they had themselves landed in the previous year (see Fig. 5). Despite this changed emphasis, their catch per unit effort was much less than in 1946-47 (see Table 11).

Table 7 also shows that there was a marked scarcity of IV+ age-group fish in the landings of 1947-48 compared with those of 1946-47. As the steam trawlers contributed very little to the landings of fish of the IV+ age group in 1946-47 it may be presumed that their landings of this group were again small in 1947-48. The reasons for this presumption are given above. The shortage therefore was felt mostly by the Danish seiners but the reason for it is not known. The shortage could not have been the result of selection by the fishermen when sorting fish for market, because the Danish seiners had landed smaller fish than in the previous year (see Fig. 5). However, it could have resulted from a poor brood year in the summer of 1943-44. On the other hand, it may only be an apparent shortage, for in 1947 some Danish seiners had commenced operating from Lakes Entrance, Vic., and as far as the author has been able to establish from the records these Danish seiners landed 1 million lb of fish in Victoria during 1947-48. This Victorian catch would not be accounted for in the New South Wales records. By adding the known Victorian catch to the New South Wales recorded landing for that year, it will be seen from

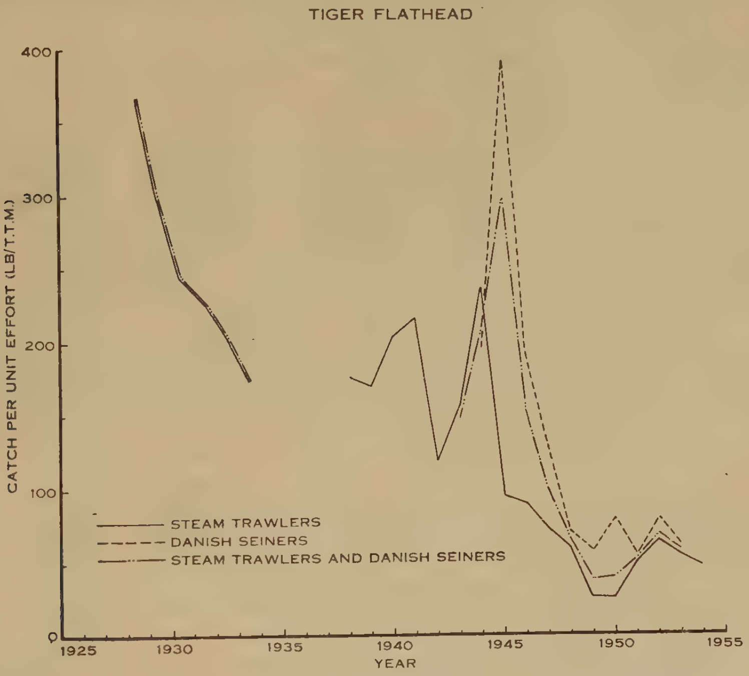

Fig. 10.—Course of the flathead catch per unit effort (lb/trawler-ton-month) for the two gears separately and the combined fleets.

Table 4 that the catch would then be remarkably close to the total for the year 1946-47. However, it has yet to be determined whether the population of tiger flathead off Lakes Entrance is part of the New South Wales stock.

Table 7 also shows that there was a shortage of the IV+ age-group fish in 1948-49. It will be remembered that the estimated numbers of fish of each age group for 1948-49 given in Table 7 are low because approximately 10 per cent. of the landed catch was omitted from the calculations. Even allowing for this error, there was a definite scarcity of IV+ age-group fish in that year compared with 1946-47. Figure 5 shows that both steam trawlers and Danish seiners were landing fish of the lower size groups in 1948-49 (see modes at 33 cm in length frequency polygons for both gears), so once again selection by the fishermen can be ruled out as a possible reason for the shortage, but it could be accounted for by again postulating a poor brood year in 1944-45.

If the Lakes Entrance tiger flathead were found to be part of the New South Wales stock, however, another explanation might account for the shortage of IV+ fish in New South Wales waters in 1948-49. The legal minimum length for tiger flathead in Victoria is only 10½ in. (cf. New South Wales, 13 in.), which would embrace fish in the II+ and III+ age groups (see Fig. 7, 1954 age-group polygons); and since some Danish seiners had fished off Lakes Entrance in 1947-48, they could legally have landed III+ age-group fish in that year. Hence fishing mortality on fish of the III+ age group in 1947-48 could have accounted in part for the shortage of IV+ age-group fish along the New South Wales coast in 1948-49.

As well as the relative paucity of IV+ age-group fish in 1948-49 there was also a scarcity of V+ age-group fish, i.e. a carry-over from the probable poor brood year of 1943-44. These relative shortages would partly account for the lowered catch (lb) and the lowered catch per unit effort for both gears in 1948-49.

Even allowing for the fact that steam trawlers landed more of the smaller fish in 1949-50 (cf. length frequency polygons for 1948-49 and 1949-50, Fig. 5) their catch and catch per unit effort remained about the same as in the previous year. Using the results in Table 7 as a guide, it would not seem unreasonable to assume: that there were poor landings of VI+ age-group fish in 1949-50; that less V+ age-group fish were landed than in 1946-47 or 1947-48; and that there were distinct declines in landings of VII+ and VIII+ age-group fish.

Table 11 shows that the catch per unit effort for the combined fleets was slightly higher in 1949-50 than in the previous year, and was higher for the Danish seiners than for the steam trawlers in 1949-50. The possibility that the better catch per unit effort for the Danish seiners was owing to landings of V+ and higher age-group fish has just been ruled out. It would seem therefore that the relative superiority of Danish seiners in 1949-50 can only be accounted for by improved landings of either III+ or IV+ age-group fish.

In 1950-51 the catch per unit effort for the combined fleets increased to 52 lb/T.T.M. and that of the steam trawlers showed an improvement over the previous year, whereas that of the Danish seiners showed a decline. The following hypothesis could account for the conditions of 1949-50 and 1950-51.

The improved landings of IV+ age-group fish made by the Danish seiners in 1949-50 was owing to a good brood year in 1945-46 which would probably give improved landings of V+ age-group fish in 1950-51. If there had been a good brood year in 1946-47 also, giving rise to good landings of III+ age-group fish in 1949-50 and good landings of IV+ age-group fish in 1950-51 (note secondary mode at 34 cm in length frequency polygons for 1950-51, Fig. 5, which would point to an influx of IV+ age-group fish; see also mode for IV+ age-group fish, Fig. 7, which corresponds to a fish length of 34 cm), the consequent benefits of these good brood years could have accounted for the improved catch per unit effort in 1949-50 for Danish seiners and in 1950-51 for steam trawlers. To account in part for the decline in catch per unit effort for Danish seiners in 1950-51 a poor brood year in 1947-48 is postulated which would give rise to poor landings of III+ age-group fish in 1950-51.

It is appropriate to consider now what further effects the products of these good brood years would have on the landings in later years. The 1951-52 catches per unit effort, for the combined fleets and for the separate gears, all showed an increase from 1950-51. Allowing for the benefits accruing from the good brood year material, i.e., V+ and VI+ fish, and allowing further for reduced fishing mortality in 1950-51 (fishing effort in 1949-50 was 53,000 T.T.M. and in 1950-51 48,000 T.T.M., a reduction which is accounted for by the reduction in size of the Danish seiner fleet; see Table 11), the all-round improvements in catch per unit effort in 1951-52 can be explained qualitatively but not quantitatively.

The year 1952-53 witnessed a decline in catch per unit effort for the combined fleets compared with the previous year. This can be attributed in part to the effects of the poor brood year of 1947-48, i.e. paucity of V+ age-group fish. Another probable factor which may be inferred is the effect of a poor brood year in 1948-49, giving rise to relatively poor catches of IV+ age-group fish in 1952-53 (note in Fig. 5 the relatively steep right-hand arm of the length frequency polygon for Danish seiners in 1952-53 compared with 1951-52).

In 1952-53 the fishing effort was higher than in the previous year (see Table 11), so that the consequent increased fishing mortality in that year would presumably decrease the relative availability of fish of the IV+ and higher age-groups in 1953-54, and this would explain in part the decline in catch per unit effort for the steam trawlers in 1953-54 (see Table 11). It must be remembered too that the effects of the poor brood years of 1948-49 and 1947-48 would be felt in 1953-54. The right-hand arms of the frequency polygons for 1953-54 in Figure 5 are steeper than those for the previous year and this would support the above explanation.

(*f*) *Summary Analysis of the Course of the Tiger Flathead Fishery*

In Section III(*a*) it was suggested that an examination of the past changes in availability of tiger flathead would be likely to indicate the remedial measures which should be adopted to improve the production of fish from the present tiger flathead stock, and so bring some measure of relief to the present poor condition of the trawlfishery as a whole.

The material for such an examination has been shown to be incomplete. However, certain salient features revealed by an interpretation of the limited data allow the formulation of some tentative conclusions.

Figure 2 and Table 4 show that following the period of reduced fishing intensity in the early and mid thirties, there was a slight improvement of tiger flathead catch and catch per unit effort. The catch had dropped slightly by 1939-40 because a section of the fleet had been requisitioned for wartime duties, but catch per unit effort continued to improve (see Table 11). Similarly in 1940-41 the fleet decreased in size, the landed catch was less than the previous year, and again the catch per unit effort improved.

There is no need to postulate an increase in the population size to account for the improved catch per unit effort in 1939-40. However, it is probable that the population did increase in size in the following year, owing to the accumulated benefits consequent on the reduced fishing effort and fishing mortality in 1939-40.

If the stock continued to increase in size, as would be expected, during the remaining war years when fishing intensity and consequently fishing mortality were relatively lower than in 1939-40, it might well be asked why there was no apparent improvement in landed catch in 1944-45 to 1946-47.

Theoretically, if the population did increase in size during the wartime rest the steam trawler catch per unit effort in the immediate post-war years should have been in the region of at least 216 lb/T.T.M., as it was in 1940-41 when the population size would be expected to be lower than in 1944-45 or 1945-46. It must be assumed therefore that the steam trawlers in 1944-45 and 1945-46 were inefficient, because their catch per unit effort was very low, approximately 90 lb/T.T.M.

It was noted earlier (Section III(*e*)) that the superiority in catch per unit effort of the Danish seiners in 1946-47 was attributable to the landings of III+ and IV+ age-group fish. Another reason for the lower catch per unit effort of the steam trawlers in 1946-47 was that they landed less numbers of the V+ and VI+ age-group fish than did the Danish seiners (cf. Tables 9 and 10) even though the fishing effort of the steam trawlers was higher than that of the Danish seiners. This would suggest that the steam trawlers were inefficient also in 1946-47.

Table 11 (see also Fig. 10) shows a pronounced superiority in catch per unit effort for the Danish seiners compared with the steam trawlers in the years 1944-45 and 1945-46. If in these two years the Danish seiners landed fish of the various age groups in the same relative proportions as they did in 1946-47, then the marked superiority could well have been the result of better landings from the Danish seiners of fish of the III+ and IV+ age groups, and relatively poorer landings of V+ and VI+ age-group fish from the steam trawlers, as was the case in 1946-47.

Unfortunately there is only limited circumstantial evidence about the size and age compositions of the catches in the pre-war years. Dakin (1939, p. 289) states that "The most usual size in the markets is probably round 38 to 40 centimetres", and Colefax (1934), summarizing the results of some 35,000 length measurements taken from March 1930 to April 1931 aboard steam trawlers during a series of 13 cruises which ranged over the main fishing areas, states that "The majority of flathead caught in 1930 fall into the 42 cm. group . . .". A length frequency curve representing these 35,000 length measurements is presented by Colefax (1934). There are four modes in the curve; the major one is at 42 cm, and there are secondary modes at 54, 32, and 24 cm, in that order of magnitude. This evidence would suggest, therefore, that the landed catches in the pre-war years from steam trawlers contained a relatively greater proportion of V+ and higher age-group fish (see Fig. 7 for age group corresponding to 38-42 cm size fish) than did the catches in 1946-47.

It is suggested at this stage that if the fishing effort in 1944-45 and 1945-46 had been wholly or in the main from steam trawlers, with the relative efficiency of each unit the same as in 1939-40, more advantage could have been taken of the improved stock.

It must be assumed that for some reason the Danish seiners were not capable of exploiting the whole of the improved stock in 1944-45 and 1945-46, otherwise the landed catches in those years should have been higher than those recorded in Table 4, and in fact higher than in the years 1937-38 to 1939-40. It follows that the low catch per unit effort for the steam trawlers could not be wholly explained by the Danish seiners having taken more than their share of the V+ and higher age-group fish. The author is at a loss to explain the inefficiency of the steam trawlers in 1944-45 and 1945-46.

To account for the unexpectedly low landings in 1944-45 and 1945-46 it is considered therefore that there was underfishing in that the Danish seiners and steam trawlers had not made the best use of the available V+ and higher age-group fish.

The low landed catch in 1946-47 now has to be accounted for. In that year the fishing effort was higher than it had been at any time in the past (see Table 11). The size of steam trawler fleet and its fishing effort were almost as great as in 1939-40, yet in 1946-47 the steam trawlers landed only 2 million lb of tiger flathead, compared with 6 million lb in 1939-40 (see Table 4).

From the circumstantial evidence mentioned earlier it would seem that there had been a falling off in fish size in the year 1946-47 compared with the pre-war years, and this would explain in part the reduced catch and catch per unit effort in 1946-47 as compared with 1939-40. If the Danish seiners in 1944-45 and 1945-46 landed fish of the various age groups in the same relative proportions as in 1946-47 (this was inferred earlier), then by taking a comparatively heavier toll of the III+ and IV+ age-group fish than in the pre-war years the reduced catch and catch per unit effort in 1946-47 could be attributed also, in part, to the fishing mortality inflicted on these age groups, resulting in a reduction in the relative availability of IV+, V+, and VI+ age-group fish in 1946-47.

TABLE 12

COMPARISON OF THE STATE OF THE FLATHEAD POPULATION IN CERTAIN PERIODS

Year	Probable Relative Density of Population at End of Year	Population Growth Trend	Fishing Effort Trend
1937-38	P_1	Steady	Steady
1938-39	$P_2 \equiv P_1$	Rising	Steady
1939-40	$P_3 > P_2$	Rising	Falling
1940-41			
1941-42			
1942-43			
1943-44	$P_7 > P_3$	Falling	Rising
1944-45			
1945-46			
1946-47	$P_{10} < P_7 < P_3 < P_2$		
1947-48			
1948-49	$P_{12} < P_{10}$	Rising	Falling
1949-50			
1950-51			
1951-52	$P_{15} > P_{12}$		
1952-53	$P_{16} < P_{15}$	Falling	Rising
1953-54	$P_{17} < P_{16}$		
1954-55*	$P_{18} < P_{17} < P_{16}$		

* Prediction.

Owing to the nature of the limited amount of available data it would be difficult, if not impossible, to resolve and evaluate quantitatively the causes underlying the fluctuations in population level from 1937-38 to the present day. A somewhat simplified qualitative expression of the state of the population at certain periods is given, however, in Table 12.

Commencing at the end of 1937-38 with the population at size P_1 it has been shown that in 1938-39 the landed catch, fishing effort, and catch per unit effort were practically the same as in 1937-38. It is therefore assumed that the population level at the end of 1938-39 was the same as at the end of 1937-38, i.e. $P_2 = P_1$. In 1939-40 the landed catch and fishing effort were less than in 1938-39, but catch per unit effort showed some improvement. The population level at the end of that year would be expected to be higher than in the two previous years, i.e. $P_3 > P_2$, since fishing mortality was lower in 1939-40.

The population was subjected to less fishing effort in 1940-41, as most of the fleet had been taken over for wartime duties, and the landed catch was lower than in 1939-40, but once again there was an increase in catch per unit effort. During the remaining war years, when fishing mortality was relatively low, the population would be expected to increase in size.

The low production in the war years was the result of underfishing; therefore at the end of 1943-44 the population would be expected to be at level P_7, with $P_7 > P_3$.

It has been suggested that the unexpectedly low landing in 1944-45 was the result of the relative inefficiency of the steam trawlers and of the inability on the part of the Danish seine fleet to exploit advantageously the V+ and higher age-group fish, and that there had been a falling off in fish size in the landed catch from Danish seiners compared with the pre-war years, when the fishing units were mostly steam trawlers.

The same reasons may account in part for the lower than expected landings in the following two years. In addition, however, relatively less IV+ and V+ age-group fish would be expected in 1945-46 than in 1943-44 or 1944-45, owing to an apparently unprecedented fishing mortality of III+ and IV+ age-group fish in 1944-45. Similarly, with further fishing mortality of the III+ and IV+ age-group fish in 1945-46 there would be relatively fewer IV+, V+, and VI+ age-group fish available in 1946-47 than in 1943-44, 1944-45, or 1945-46. Therefore the population level P_{10} at the end of 1946-47 would probably be lower than the level P_7 of 1943-44 and lower than 1944-45 or 1945-46, with $P_{10} < P_7$.

There appear to have been three main causes for the decline in catch and catch per unit effort for both fleets in 1948-49, viz.

(i) the carry-over effect of a probable poor brood in 1943-44;

(ii) the further unprecedented fishing mortality of the lower size groups by the Danish seiners in 1947-48;

(iii) the effect of a probable poor brood in 1944-45.

In 1948-49 the effects of these adverse changes were apparently being felt mostly by the Danish seiners because some of them had moved out of the industry (see Table 3). The steam trawlers, however, were able to supplement their low catches of tiger flathead with landings of morwong and nannygai (see Tables 5 and 6).

As fishing effort decreased during the period 1948-49 to 1951-52 and as there would seem to have been two good brood years in 1945-46 and

1946-47, it can be assumed that the population increased up to the end of 1951-52.

It would appear, however, that the improved catch and catch per unit effort in 1951-52 (see Tables 4 and 11) attracted further fishing units into the fishery in 1952-53. The consequent increased fishing effort, coupled with the probability that there had been poor broods in 1947-48 and 1948-49 (see Section III(*e*)), resulted in a decline in catch per unit effort in 1952-53 even though a greater weight of tiger flathead was landed in that year than in 1951-52 (see Table 4).

It would be reasonable to assume that owing to increased fishing mortality in 1952-53 (consequent on the increased fishing effort), and the poor brood years of 1947-48 and 1948-49, the population level was lower at the end of 1952-53 than at the end of 1951-52, i.e. $P_{16} < P_{15}$.

Since the fishing effort in 1953-54 was higher than in 1952-53 (see estimated total in Table 7), and as the catch and catch per unit effort fell for steam trawlers (see Tables 4 and 11), and probably for Danish seiners (estimate based on data in Table 10), the population level at the end of 1953-54 would probably be lower than at the end of 1952-53, i.e. $P_{17} < P_{16}$.

Provided the fishing effort remains the same in 1954-55 as in 1953-54, the prospects for 1954-55 are not particularly bright, unless there was an exceptionally good brood in 1950-51, and the industry can anticipate a further decline in landed catch and catch per unit effort, and a population level at the end of 1954-55 lower than at the end of 1953-54, i.e. $P_{18} < P_{17}$.

IV. Discussion

The overall general course of the trawlfishery was dealt with briefly in Section II(*c*), and was illustrated in Figure 1. This figure shows that at the time of writing the trawlfishery as a whole is experiencing a period of relatively poor fishing in respect of catch per unit effort, for all species. A very similar condition was witnessed in the mid thirties, which was mainly the result of reduced landings of tiger flathead. During the early thirties other species of fish (e.g. morwong and nannygai) were landed to supplement the reduced catches of tiger flathead, and by the late thirties there were signs of improvement. This resulted partly from increased landings of other species and partly from relatively better landings of tiger flathead (see Fig. 2, which shows this for steam trawlers). Since the data are scanty it can only be inferred that this evidence of change in the tiger flathead stock was the result of the antecedent reduction of fishing effort in the early thirties.

It would seem, however, that the present condition cannot be improved by resorting to landings of other species as was done in the late thirties. The morwong catch and catch per unit effort are showing signs of deteriorating again (see Fig. 11), and this would tend to counterbalance the recent slight upward trend of catch and catch per unit effort for nannygai (see Fig. 12).

In the absence of regulative measures and under the stress of the existing intensity of fishing effort, no improvement can be expected from the tiger flathead stock (see Section III(*f*)).

To bring about an improvement of the existing catch and catch per unit effort it would seem that the only course is to introduce management measures.

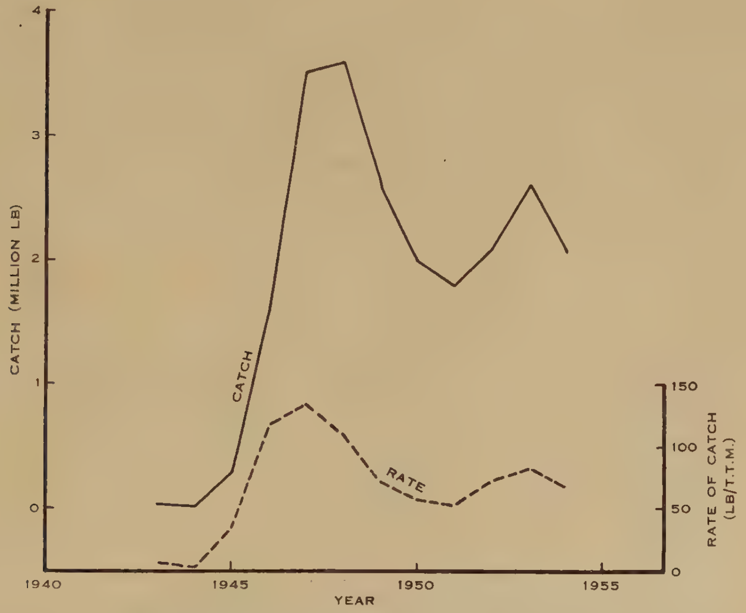

Fig. 11.—Morwong catch and catch per unit effort (lb/trawler-ton-month), for steam trawlers only.

Fairbridge (1948, 1952) expresses the belief that the limitation of the fleet to approximately 3000-3500 trawler-tons would be highly desirable, since at that level in the mid thirties the tiger flathead catch and catch per unit effort were showing signs of recovery. This proposal, if implemented, would be expected to give some measure of relief as the catch per unit effort would almost certainly improve. However, further management measures would need to be introduced to improve the total catch of tiger flathead, and these measures should be aimed at improving fish size. Such an improvement could not be expected by sorting out fish after they have been caught. It is well known on the New South Wales coast that when tiger flathead are brought up from the trawling grounds and landed on deck, the majority die in a very short time. To return undersized fish to the water after they are landed on board, even though they may be quite active, is also known to be a wasteful practice, since the fish, having been subjected to reduced pressure with consequent inflation of their air bladders, become easy prey for birds and sharks when returned to the sea.

A little work, involving covered cod-ends, has been done to determine a suitable Danish seine cod-end mesh size which would allow the escape of tiger flathead smaller than 33 cm in length. The results indicate that for Danish seiners a cod-end having meshes of 3¼ in.* could act as a savings device and give a 50 per cent. selection point very close to the existing New South Wales legal size of 33 cm (13 in.).

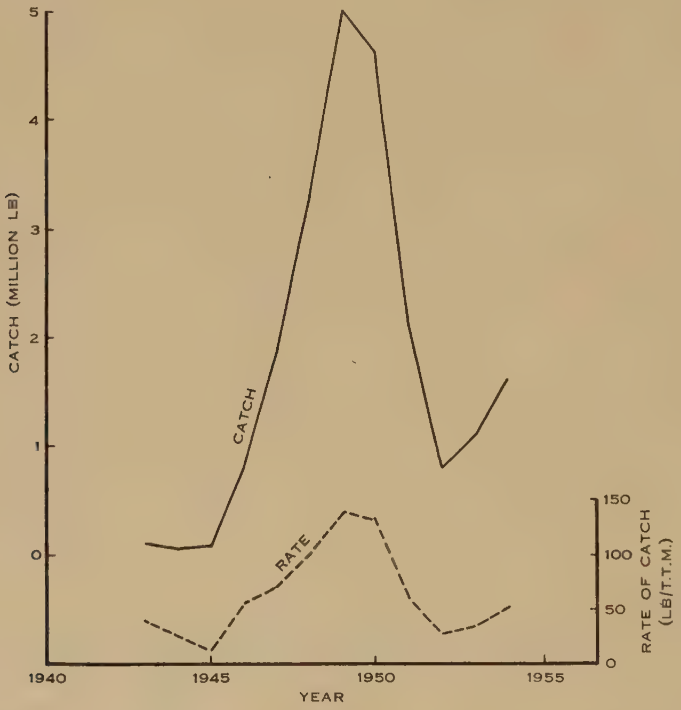

Fig. 12.—Nannygai catch and catch per unit effort (lb/trawler-ton-month), for steam trawlers only.

So far it has not been possible, owing to lack of sea-going facilities, to carry out similar tests with steam trawl gear. However, judging by reports (e.g. Lucas 1954) from the United Kingdom on the results of comparative selectivities of trawl and seine nets which showed that the seine mesh size should be slightly less than that of the trawl to give equivalent conservation results, it seems likely that the steam trawl cod-end mesh size in New South Wales waters would have to be 3½ in. to give results comparable with those mentioned above for Danish seine gear.

To derive a more exact interpretation of the status of this important fishery, or to predict the reaction of the fish populations to any management measures which may be introduced in the future, it would be necessary to bridge many gaps in the existing knowledge. This paper and those by Fairbridge reveal the difficulties of attempting to discover and locate the adverse changes in the trawlfishery by studying only statistics and market samples. It would have been very useful, for instance, to have had knowledge of the proportion of the three main species in the catches from different localities.

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* Inside mesh measurement, i.e. distance between top and bottom knots, with these knots fully drawn apart and side knots in contact, for a wet net in use.

Owing to lack of information on locality data from the steam trawler catches, it is impossible to determine whether or not there has been some selective fishing since the war. It is possible, for example, that to supplement their low catches of tiger flathead, the steam trawlers have concentrated more on grounds giving better catches of morwong and nannygai and relatively poorer catches of tiger flathead. Until the Australian investigators have a vessel to fish alongside trawlers and Danish seiners, enabling them to formulate and test their hypotheses immediately in the field, further progress is bound to be slow.

V. ACKNOWLEDGMENTS

The writer's thanks are due to Dr. M. Blackburn, Division of Fisheries, C.S.I.R.O., for constant interest shown in the trawlfishery problems, and for much helpful advice and criticism of the manuscript. He is particularly indebted to Mr. John Woore of the State Fisheries Branch for maintaining the sampling programme at the Sydney Fish Market. The help of officers of the New South Wales Fisheries Branch and the Maritime Services Board in supplying fisheries statistics is gratefully acknowledged.

The writer wishes to thank Mr. R. Breach, Division of Fisheries, C.S.I.R.O., for help in preparing the figures and Mr. I. S. R. Munro of the same Division for helpful discussion.

In many ways this paper is based on the groundwork and methods laid down by Mr. W. S. Fairbridge before his death in May 1950, and this is an opportune time to record a tribute.

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LITTORAL PENAEINAE FROM NEW SOUTH WALES AND ADJACENT QUEENSLAND WATERS

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(*Manuscript received November* 30, 1954)

Summary

The taxonomy of the subfamily Penaeinae has been revised and coordinated with the latest results of overseas workers, following chiefly Burkenroad's systematic groupings. A key to groups, genera, and species is given for Penaeinae occurring in Australian waters and the adjacent part of the Indo-Pacific region, with special reference to those on the east coast of Australia. Sixteen species occurring in commercial catches off New South Wales and southern Queensland are fully described, and 11 illustrated.

I. INTRODUCTION

In view of the rapid growth of the penaeid prawn fisheries in New South Wales, especially in ocean waters since 1948, special prawn investigations were initiated in 1951 by the Chief Secretary's Department in response to expressed concern over the possibility of depletion of the stocks. Since May 1953, comprehensive studies have been carried out on their biology, ecology, and embryology. Some centres of commercial prawn fisheries have been investigated in detail, especially along the far north coast of New South Wales.

During these biological investigations it became imperative to revise and coordinate the hitherto rather badly confused taxonomy of a quite considerable number of species of commercial penaeid prawns. Since Haswell's (1879, 1882) publications on this group, there has been no revision of the Australian forms except in Schmitt's (1926) excellent *Endeavour* report; however, the nomenclature of individual species has been commented on by several Australian writers. A review of the genera and species, together with a comprehensive key in line with Burkenroad's (1934*a*, 1934*b*, 1939) revisions and seriations, therefore appears highly desirable.

This paper does not attempt to give more than a preliminary account of the long neglected taxonomy of Australian commercial species, for some nomenclatural problems will still remain, but it is hoped that it will stimulate other workers here and abroad to combined efforts in clearing up the remaining problems on an international cooperative basis, particularly as the status of the Indo-Pacific genera and species of the *Trachypeneus* group in Burkenroad's sense appears to demand a thorough revision.

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The species discussed were collected during extensive field trips aboard commercial vessels from various parts of the New South Wales coastline and adjacent Queensland waters, including Moreton Bay (see Fig. 1). The gear used for their capture was the otter trawl, and experimental baited traps, the latter chiefly at depths of over 50 fathoms.

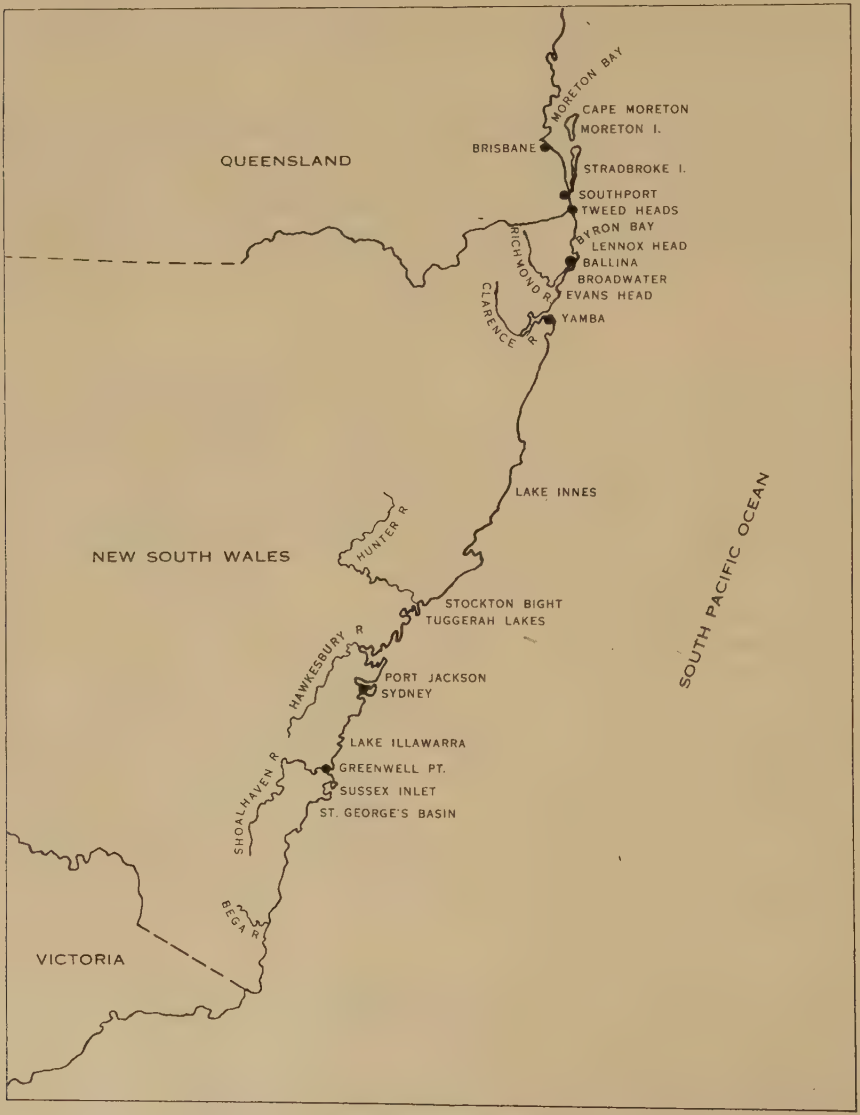
QUEENSLAND
MORETON BAY
CAPE MORETON
MORETON I.
BRISBANE
STRADBROKE I.
SOUTHPORT
TWEED HEADS
BYRON BAY
LENNOX HEAD
BALLINA
BROADWATER
EVANS HEAD
YAMBA
RICHMOND R
CLARENCE R
LAKE INNES
NEW SOUTH WALES
HUNTER R
STOCKTON BIGHT
TUGGERAH LAKES
HAWKESBURY R
PORT JACKSON
SYDNEY
LAKE ILLAWARRA
GREENWELL PT.
SUSSEX INLET
ST. GEORGE'S BASIN
SHOALHAVEN R
BEGA R
VICTORIA
SOUTH PACIFIC OCEAN

Fig. 1.—Area of field investigations.

To avoid possible misrepresentation through incorrect drawings, most of the typical species and their distinguishing features, mainly thelyca and petasmas, have been photographed.

II. TAXONOMIC CRITERIA

There are many typical distinguishing features providing the main criteria of penaeine genera and species which allow of quick and reliable determination. A brief general description of these is given and their usefulness and variability discussed before a systematic account is attempted.

(*a*) *Carapace*

See Figure 2 for diagram of distinguishing features.

The shape and elevation of the rostrum is quite characteristic for certain species, although only of secondary diagnostic value because of considerable variations within the species, as well as ecomorphic alterations. Particularly, the number of rostral teeth is very variable within species, but there is always a more or less constant mode which is helpful in diagnosis.

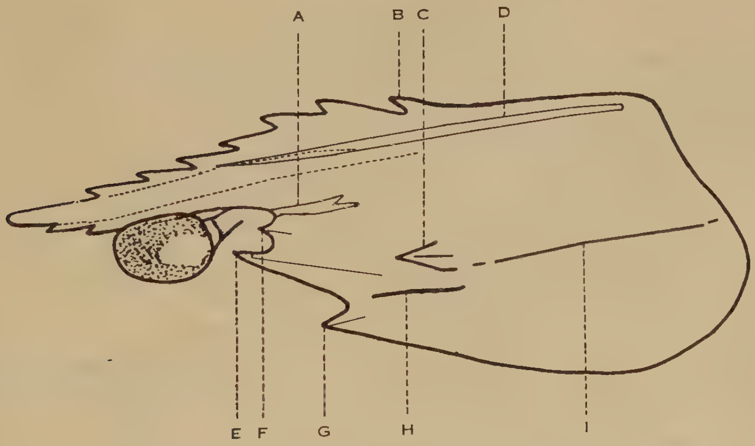

Fig. 2.—Distinguishing features of carapace. *A*, post-ocular crest; *B*, epigastric tooth; *C*, hepatic spine; *D*, lateral grooves; *E*, antennal spine; *F*, postocular (orbital) spine; *G*, pterygostomian (branchiostegal) spine; *H*, subhepatic crest; *I*, posthepatic crest.

The length, shape, and sometimes width of the adrostral and median sulci are very helpful features, together with the presence or absence of a postrostral carina and postocular crest. The looping of the latter, being constant and characteristic within the species of "grooved prawns" (*Penaeus plebejus* and its relatives), is of high diagnostic value.

Another criterion of specific usefulness is the shape, direction, length, and prominence of the subhepatic crest, if present. This crest may be strongly defined or just discernible, appearing as a narrow linear groove; it may be parallel to the axis of the carapace, or forming an angle with it, and it may be straight or arcuate. In fact, the subhepatic ridge is a most valuable distinguishing feature in the *Penaeus* group, especially when dealing with damaged specimens, chiefly those with missing pereiopods and petasmas.

The presence or absence of fissures (longitudinal, transverse, or both) on the carapace, and their length and position are very useful characters, and also the presence and position of a pterygostomian (branchiostegal) spine. Stridulating ridges on the posterolateral margin of the carapace are characteristic for *Penaeopsis* (*Metapenaeopsis*) *novae-guineae*, and the prominence and length of the posthepatic carinae are of distinguishing value amongst species of *Metapenaeus*, being quite constant.

The pubescence is a specific character in *Metapenaeus*; the carapace may be almost smooth to finely tomentose, with pubescence in shallow grooves or wide irregular patches. The presence or absence of pubescence on the rounded marginal area between the rostrum and the postocular (orbital) tooth, a character not previously described, is also of diagnostic value in *Metapenaeus*.

(*b*) *Abdomen*

The carination of the pleonic segments has some diagnostic value, but the most useful criteria are the amount and pattern of pubescence and the presence or absence of spines on the telson.

The differentiation of *Metapenaei* with numerous but very minute spinules on the telson (often commented on as "telson unarmed") is very difficult without a detailed study of their genitalia. However, the position and pattern of pubescence, so typical for most of the species of *Metapenaeus*, prove to be constant specific characters with negligible variations, and are of valuable secondary use.

Furthermore, the arrangement of pubesence on the sternum of the sixth pleonic segment is of specific significance in *Metapenaeus*. This is a character which has not been noted by previous writers. The sternum may be glabrous, or may bear anteriorly one to three linear, longitudinal rows of pubescence. On the posterior third of the sternum there is an ellipsoid, more or less setose elevation, which has a peculiar "streamlined" shape throughout the species of *Metapenaeus*. The sternal area, bordering its distal rounded margin may be naked, or may bear transverse rows of setae, a useful character quite constant within the species.

A characteristic generic and specific criterion is the telson, which may be unarmed, or may bear numerous minute spinules, or may be armed with movable or fixed spines, or a combination of both. The variation of this character within the species is negligible.

(*c*) *Appendages*

Amongst the cephalic appendages, the presence or absence of a spine on the ventromedian margin of the basal segment of the antennular peduncle is a generic character of great value. As noted by Alcock (1906), and later by Schmitt (1926), the length of the dactylus of the third maxillipeds in relation to the length of the propodus in male adults is of great importance in the otherwise quite difficult differentiation of species in the *Penaeus indicus* group.

Furthermore the presence or absence of spines on the basis and ischium of the chelipeds, the presence or absence of exopodites and epipodites on some of the pereiopoda, and to some extent the length of the latter are useful criteria. In *Parapenaeus*, however, the exopodites may be reduced to hardly discernible rudiments, and are often commented on as being absent (Barnard 1950, key). The length of the pereiopods varies greatly with the growth of the individual, and is to be regarded only as a strictly adult character.

(*d*) *Genitalia*

Above all other criteria, the thelycum and the petasma will always provide the best adult characters for diagnostic purposes. The shape and position of the lateral plates and the structure and size of the median plate are excellent generic and specific distinguishing features, together with coxal modifications on the fourth and sometimes the third pereiopoda.

The adult petasma also provides the best distinguishing features and, especially in differentiation within the genus *Metapenaeus*, its characters are of decisive value. Moreover, modifications of the male pereionic sterna and fifth pereiopoda, as well as the structure of the appendix masculina on pleopod 2, are very useful for generic differentiation.

It is unwise, however, to attempt specific differentiation upon characters of one sex only, and a range of samples is desirable. Especially when dealing with species of the *Metapenaeus monoceros* group, ecomorphic alterations and modifications have to be taken into consideration, changes which may affect one sex more than the other.

(*e*) *Colour in Life*

Coloration, and especially colour patterns, are criteria of important diagnostic value, and it is to be regretted that they are so seldom taken into consideration. Observations in the field on live, or at least fresh, samples are far superior to studies of collections kept in preservatives over a longer period.

In general, coloration of the body and appendages may vary with growth and environment; the same species may be translucent-greenish in juvenile stages and become later, as an adult, pink, yellow, or reddish. However, the colour pattern on carapace, abdomen, antennae, and sometimes even on pereiopoda, pleopoda, and uropoda, is quite stable, even when the colour value is subject to variations. *Metapenaeus incisipes*, for example, has typical striped pereiopoda, varying from red-white to orange-cream in both sexes, and can thus be distinguished at a glance from other species of the group. Disregarding other important criteria and different coloration, *Penaeus esculentus* can be readily distinguished from *Penaeus* *carinatus* by the pronounced and characteristic colour pattern on the carapace, which in the latter remains always quite obscure.

III. TAXONOMY

Family **PENAEIDAE** Bate

Subfamily **PENAEINAE** Burkenroad

KEY TO GROUPS OF THE SUBFAMILY PENAEINAE

1. Ventral rostral teeth present in all of the species of all genera (except in subgenus *Funchalia*). Epipodite present on the 3rd maxillipeds. Pleurobranch present on somite 14 .... *Penaeus* group

Ventral rostral teeth absent. Epipodite absent on 3rd maxillipeds. No pleurobranch on somite 14 2

2(1). A distal fixed pair of spines on the telson (telson trifid), and 1-3 pairs of mobile lateral spines. Basal segment of antennular peduncle medially with a spine .... *Parapenaeus* group

No distal fixed pair of spines on the telson (telson not trifid), but mobile lateral spines may be present in variable number. Basal segment of antennular peduncle medially without a spine 3

3(2). Pereiopoda without exopodites behind somite 10; anterior legs without a spine on ischium .... *Macropetasma* group*

Pereiopoda with exopodites behind somite 10; anterior legs armed with a spine on ischium .... *Trachypeneus* group

The *Penaeus* group, as defined by Burkenroad (1934*a*), consists of the genera *Penaeus* Fabricius, *Heteropenaeus* De Man, and *Funchalia* Johnson. Since the latter two genera have not been recorded from Australian waters, their definition is here omitted.

Genus PENAEUS Fabricius

KEY TO AUSTRALIAN AND INDO-PACIFIC SPECIES OF THE GENUS PENAEUS FABRICIUS

1. Lateral grooves on the carapace not extending posterior to the gastric tooth. Rostrum with 2-5 teeth on ventral edge. Telson without lateral spines. Postocular crest absent 2

Lateral grooves on the carapace extending almost to the posterior margin of carapace. Rostrum with only 1 tooth on ventral edge (except *P. marginatus*). Postocular crest present 8

2(1). Carapace with more or less prominent subhepatic crest 3

Carapace without subhepatic crest 7

3(2). Fifth pair of pereiopoda without exopodites. Rostral formula usually 7/3. Subhepatic crest very prominent, reaching well behind hepatic spine. Postrostral carina flat-topped with indications of a sulcus 4

Fifth pair of pereiopoda with small but well-formed exopodites. Subhepatic crest not very prominent 5

4(3). Median plate of thelycum posteriorly with prominent longitudinal crest. Colour in life dark buff, with dark grey crossbands ...... *P. carinatus* Dana

Median plate of thelycum posteriorly with V-shaped ridge. Colour in life vivid blue, with darker blue crossbands .... *P. caeruleus* Stebbing

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* Not occurring in Australian waters.

5(3). Postrostral carina distinctly sulcate. Rostral formula 6-7/3. Subhepatic crest formed by an oblique incision, extending from a little behind the hepatic spine toward the antero-inferior angle of carapace ......*P. semisulcatus* de Haan
Postrostral carina not sulcate 6

6(5). Rostral formula 5-7/3-4, rostrum quite straight, except for a light upturning of the tip. Subhepatic crest formed by a short linear incision, not extending behind antennal sulcus-ridge angle ....*P. esculentus* Haswell
Rostral formula 9/2. Subhepatic crest longitudinal and arcuate, extending somewhat behind antennal sulcus-ridge angle ....*P. gracilirostris* Thallwitz

7(2). Rostral crest of moderate height, rostrum often exceeding the antennal scale. Anterior dorsal rostral tooth placed at most over terminal segment of antennular peduncle. Adrostral sulci somewhat exceeding the gastric tooth. Dactyl of 3rd maxillipeds of adult male about as long as propodus ....*P. indicus* Milne Edwards
Rostral crest very high and assuming a triangular shape, rostrum about as long as antennal scale. Anterior dorsal rostral tooth usually placed in advance of terminal segment of antennular peduncle. Adrostral sulci not quite reaching gastric tooth. Dactyl of 3rd maxillipeds of adult male scarcely half as long as propodus ....*P. merguiensis* De Man
Rostral crest high, but not assuming a triangular shape, rostrum about as long as antennal scale. Dactyl of 3rd maxillipeds of adult male about twice the length of propodus ....*P. penicillatus* Alcock

8(1). Telson without lateral spines ....*P. canaliculatus* Olivier
Telson with 3 pairs of lateral spines 9

9(8). Ischium of 1st pereiopoda armed ....*P. marginatus* Randall
Ischium of 1st pereiopoda unarmed 10

10(9). Rostrum without a secondary or accessory pair of lateral grooves. Postocular crest forming single loop 11
Rostrum with a secondary or accessory pair of lateral grooves. Postocular crest forming double loop 12

11(10). Thelycum tubular, the 2 lateral halves indistinguishably fused. Petasma with submedian "horns" bent over, overhanging distal margin of side plates ....*P. japonicus* Bate
Thelycum composed of 2 distinct plates, not fused medially. Petasma with submedian "horns" only slightly bent over, not overhanging distal margin of side plate ....*P. latisulcatus* Kishinouye

12(10). Lateral grooves paralleling medially sulcate postrostral carina not confluent near posterior margin of carapace ....*P. plebejus* Hess
Lateral grooves paralleling medially sulcate postrostral carina confluent near posterior margin of carapace, forming an X-shaped depression ....*P. maccullochi* Schmitt

PENAEUS CARINATUS Dana

Plate 1, Fig. 1; Plate 2, Figs. 1, 2; Plate 5, Fig. 1; Plate 8, Fig. 1

? *Penaeus monodon* Fabricius, 1798, p. 408.

Penaeus carinatus Dana, 1852, p. 602, pl. 40, fig. 2. De Man, 1911, p. 101. Kemp, 1915, p. 317, fig. 36. Burkenroad, 1934*a*, p. 74. Anderson and Lindner, 1943, p. 305.

Penaeus monodon Haswell, 1882, p. 199. Kishinouye, 1900, pp. 7, 15, pl. 2, fig. 1; pl. 7, figs. 3, 3*a*. Stebbing, 1910, p. 380. Boone, 1935, p. 87, pl. 22, fig. 5. Barnard, 1950, p. 584, figs. 107*a-f*.

Peneus semisulcatus Alcock, 1906, pp. 8, 10-11, pl. 1, fig. 2 (non de Haan, 1850).
Peneus carinatus Schmitt, 1926, pp. 359, 363.

Vernacular names: tiger prawn, jumbo prawn, giant tiger prawn.

Rostral formula usually 7/3, range 6-8/3-4. Rostrum distinctly double-curved, extending to end of antennal scale. Lateral grooves not exceeding the hindmost rostral tooth. Postrostral carina almost reaching the posterior margin of carapace, flat-topped with indications of a sulcus (mostly 2 shallow elongated depressions). Carapace smooth and thick. Subhepatic ridge very prominent, longitudinal and slightly arcuate, extending posteriorly from one-half to one-third of its length behind the angle formed below the hepatic spine by the meeting of the antennal sulcus with the ridge pointing to the antennal spine. Exopodites are absent from the 5th pair of pereiopoda, an immobile papilla marking their position. Abdominal segments 4-6 dorsally keeled, keel on somite 6 ending acutely. Telson without lateral spines.

The lateral plates of the thelycum meet for the posterior half of their length (when fully developed), and their median rims are most prominent somewhat posterior to the insertion of the median plate. The median plate is posteriorly convex and bears a very prominent longitudinal ridge, which disappears about on a level with the anterior margins of the lateral plates.

The petasma is longitudinally folded and has short submedian protuberances.

Length up to 305 mm (12 in.).

Colour in life dark buff to olive green, speckled with blue, with conspicuous grey to black crossbands on abdomen. Colour pattern on carapace somewhat obscure. Antennal scales, eyestalks, and uropoda dark blue, fringe on uropoda reddish brown. Pleopoda dull red with blue peduncles. Antennae banded.

Material.—NEW SOUTH WALES: Off Tweed Heads, Lennox Head, Ballina, Broadwater, Yamba, Stockton Bight (12-20 fm), and Byron Bay (60 fm). QUEENSLAND: Off Southport (18 fm).

Distribution.—Indian seas, Indonesia, Philippines, Japan.

Discussion.—Owing to the obscure and insufficient description by Fabricius (1798), and to the subsequent confusion between *monodon* and *semisulcatus* by later authors, De Man (1911) and Kemp (1915) recorded this species under Dana's (1852) name. Kemp (1915) states that "De Man has not associated any species with the Fabrician name and it is probably best that it should be ignored, though the possibility that the type specimen still exists must remain a menace to the stability of the revised nomenclature. It is a choice of evils".

Haswell's (1882) description of *monodon* Fabricius is also somewhat obscure, and Kishinouye (1900), although considering *monodon* Fabricius and *semisulcatus* de Haan synonymous, figures and describes his *monodon* in a way agreeing well with *carinatus*. Bate's (1888) and Alcock's (1906) *monodon* are certainly identical with *semisulcatus* de Haan. As Fabricius' definition could refer to *semisulcatus* de Haan, to *carinatus* Dana, or even to species of the *indicus* group, Dana's name should be employed, to avoid further confusion by the reintroduction of the unstable term *monodon*.

In Australia, this species has often been confused with *esculentus* Haswell, although it is obviously distinct from the latter in many features; in particular very large specimens were considered to be adult forms of *esculentus*. Schmitt (1926, p. 365) quoted correspondence from McCulloch, recording sizes up to 12.25 in. for *esculentus*, which quite certainly refer to *carinatus*. During extensive field investigations the author was able to examine many hundreds of specimens of *esculentus*; this species rarely exceeds 8 in. in total length.

With experimental traps, large mature females were captured off the north coast of New South Wales in depths over 60 fm, together with *esculentus*.

PENAEUS CAERULEUS Stebbing

Plate 1, Fig. 3

Penaeus caeruleus Stebbing, 1905, p. 77, pl. 21, 21 *bis*. Burkenroad, 1934*a*, p. 74. Anderson and Lindner, 1943, p. 305.

Vernacular name: blue tiger prawn.

Rostral formula and ridges on carapace as in *carinatus*; the rostrum distinctly double-curved, but somewhat lower than in *carinatus*. Foremost ventral rostral tooth much closer to the apex of the rostrum, less than its distance to the following tooth. Exopodites absent from the 5th pair of pereiopoda, an immobile papilla marking their position. Telson without lateral spines.

The lateral plates of the thelycum, when fully developed, meet for the posterior two-thirds of their length, and their median rims are low and almost equal throughout their length. The median plate bears posteriorly a short but pronounced knob-like ridge, which divides in a V-shape to form the outer, raised lateral margins of the median plate. These raised lateral margins are discontinued after reaching the anterior margins of the lateral plates.

The petasma shows no characters distinctive from *carinatus*.

Length up to 280 mm (11 in.).

Colour in life vivid blue with conspicuous dark blue crossbands on the abdominal segments. There is no colour pattern discernible on the carapace. Antennal scales, eyestalks, uropoda, and walking legs greenish blue, pleopoda darker blue with bright blue peduncles. Antennae banded.

Material.—NEW SOUTH WALES: Off Ballina (18 fm), Byron Bay (20 fm), and Yamba (25 fm). QUEENSLAND: Moreton Bay (6-8 fm).

Distribution.—Previously recorded from east coast of Africa.

Discussion.—The diagnostic features of *caeruleus* separating this species from *carinatus* are scarce and, except for the slightly different structure of the thelycum, only of secondary value. The length of the antennular flagella in relation to their peduncles (Anderson and Lindner 1943, key), together with the characteristic coloration of the body, as distinguishing features alone, could certainly not justify the standing of this species. Moreover in New South Wales specimens the antennular flagella seem to be somewhat shorter than their peduncles, quite contrary to previous reports.

Barnard (1950) has no hesitation in considering *caeruleus* a synonym of *carinatus* and does not even regard it as a special colour variety. However, he gives no indications, definitions, nor descriptions for his opinion. As Burkenroad (1934*a*, p. 74) lists *caeruleus* as amongst 21 clearly characterized species of the genus *Penaeus*, the standing of this species should be retained, unless more evidence to the contrary can be collected.

This species is very rarely captured in New South Wales.

PENAEUS SEMISULCATUS de Haan

? *Penaeus monodon* Fabricius, 1798, p. 408.
Penaeus semisulcatus de Haan, 1850, p. 191, pl. 46, fig. 1. Barnard, 1950, p. 588.
Penaeus monodon Bate, 1888, p. 250, pl. 34, fig. 1.
Penaeus ashiaka Kishinouye, 1900, pp. 7-14, pl. 3.
Peneus monodon Alcock, 1906, pp. 8-10, pl. 1, figs. 1, 1*ab*.
Peneus semisulcatus Schmitt, 1926, pp. 360, 364.

Rostral formula usually 7/3. Rostrum slightly double-curved, extending to end of antennal scale. Lateral grooves on carapace not exceeding the hindmost rostral tooth. Postrostral carina almost reaching the posterior margin of carapace, postrostral sulcus distinct. Subhepatic crest not prominent, appearing as a narrow, oblique groove, running from a little behind the antennal sulcus-ridge angle in the direction of the antero-inferior angle of the carapace. This oblique "incision" forms a distinct angle with the axis of the carapace. The 5th pair of pereiopoda possesses small, but distinct non-setose exopodites. Telson without lateral spines.

Length up to 230 mm (9 in.).

Colour in life dark green with somewhat obscure darker crossbands on abdomen. The carapace has no characteristic colour pattern. Antennal scales, eyestalks, pleopoda, and uropoda dull red, the uropoda with a brownish fringe. Pereiopoda "tigered" with a characteristic yellow and reddish colour pattern. Antennae banded.

Material.—2 immature females taken in 18 fm south of Ballina, N.S.W.

Distribution.—Suez, Red Sea, India, Indonesia, Philippines, Japan; Mediterranean, by migration through the Suez Canal.

Discussion.—This species, although often confused with *carinatus* by earlier writers, is more closely related to the Australian species *esculentus* than to the widely distributed *carinatus*. Characters distinct from *carinatus* and in common with *esculentus* are: the stouter and shorter carapace; the less distinct double curve of the rostrum, resulting in an increased width of the upper blade; the structure of the subhepatic crest; and the presence and structure of the exopodite on the 5th pereiopoda.

As only 2 immature females were taken in commercial catches off New South Wales the author was unable to define possible diagnostic characters of the thelycum, which is open in both specimens, and resembles closely immature thelyca of *carinatus*.

P. semisulcatus seems to be very rare in east Australian waters.

PENAEUS ESCULENTUS Haswell

Plate 1, Fig. 2; Plate 2, Fig. 3; Plate 5, Fig. 2; Plate 8, Fig. 2

Penaeus esculentus Haswell, 1879, p. 38; 1882, p. 200. De Man, 1911, p. 96. Burkenroad, 1934*a*, p. 74.

Penaeus monodon Whitelegge, 1889, p. 224; in Ogilby 1893, p. 203 (non Fabricius (1798)).

Peneus esculentus Schmitt, 1926, pp. 360, 362, pl. 64, figs. 1-4.

Vernacular names: tiger prawn, common tiger prawn, New South Wales tiger prawn.

Rostral formula usually 7/3, range 5-7/3-4. Midrib of the rostrum quite straight throughout its length except for a slight upturning of the tip. Upper blade considerably wider than in *carinatus*. Rostrum somewhat shorter than antennal scale. Lateral grooves not exceeding the hindmost rostral tooth. Postrostral carina blunt, not sulcate, and not reaching to posterior margin of the carapace. Subhepatic crest formed by the lower margin of a short, straight longitudinal groove, extending posteriorly scarcely as far as the antennal sulcus-ridge angle. The 5th pair of pereiopoda possesses small but distinct non-setose exopodites. Telson without lateral spines.

The median margins of the lateral plates of the thelycum are very prominent and raised to form conspicuous and crenulated parallel ridges. The medium plate has anteriorly slightly raised edges and bears posteriorly a short, knob-like ridge.

The petasma is longitudinally folded and its submedian protuberances are more prominent than in *carinatus*.

Length up to 220 mm (8½ in.).

Colour in life pale buff to olive green with dark brown conspicuous crossbands on carapace and abdomen. The colour pattern on the carapace is particularly characteristic and constant (Plate 1, Fig. 2). Crest on carapace and last 3 pleonic segments dull red. Antennal scales and eyestalks olive green, uropoda brownish red. Fringe on uropoda, and pleopoda dull red. Antennae banded.

Material.—NEW SOUTH WALES: Along the whole coastline, less abundant south of Sydney. QUEENSLAND: Middle and south coast, Moreton Bay.

Distribution.—East and west coasts of Australia.

Discussion.—This well-known species, previously found only off the north and east coasts of Australia, and recently recorded even from the Dampier Archipelago, W.A., has been well characterized by Schmitt (1926). However, it has been repeatedly confused with *carinatus*, although differing from it in many characteristic features (see key and above description).

P. esculentus, the well-known tiger prawn, occurs in the inner and outer littoral area, and enters the estuarine (inside) area only occasionally. Irregular in its appearance, this species enters the commercial catch usually in the late summer months, and is then of some importance, especially on the north coast of New South Wales and in Moreton Bay, Qld. It has been also experimentally trapped by the author off the north coast of New South Wales in depths to 65 fm.

PENAEUS INDICUS Milne Edwards

Penaeus indicus Milne Edwards, 1837, p. 415. Dana, 1852, p. 604. Bate, 1888, p. 248, pl. 33, fig. 2. Boone, 1935, p. 91, pl. 23, fig. 6. Barnard, 1950, p. 588, figs. 107*g-l*.

Penaeus indicus var. *longirostris* De Man, 1892, p. 511, pl. 39, fig. 53.

Peneus indicus Alcock, 1906, p. 12, pl. 1, figs. 8, 8*a*. Schmitt, 1926, p. 361.

Penaeus semisulcatus Stebbing, 1915, p. 69 (non de Haan (1850)).

Rostral formula usually 8-9/4-5. Rostrum distinctly double-curved, slender distally, and reaching at least to, mostly exceeding, the tip of the antennal scale, being usually longer in juveniles than in adults. Rostral crest of moderate height, anterior dorsal rostral tooth placed at most over terminal segment of antennular peduncle. Lateral grooves reaching to gastric tooth, slightly exceeding the latter. Postrostral carina feebly developed, bearing 1 or 2 shallow sulci. Carapace smooth, subhepatic crest absent. Abdominal segments 4-6 distinctly carinated, keel on last segment ending acutely. Telson without lateral spines. A small but distinct non-setose exopodite on 5th pair of pereiopoda. Dactyl of 3rd maxillipeds of adult male about as long as propodus.

The lateral plates of the thelycum form together an oval pad. Their median margins are rim-like throughout their length and moderately raised. The median plate is posteriorly very narrow, forming a moderate ridge; its anterior margin is almost triangular, lance-shaped.

The petasma is much like that of *esculentus* with quite prominent submedian protuberances.

Length up to 200 mm (7¾ in.).

Colour in life pale buff (body semi-translucent) with blue pigment spots. Crest of carapace and abdomen reddish brown. Eyestalks and antennal scales bluish, margin of uropoda blue with bright red fringe. Antennae not banded, antennulae spotted.

Material.—NEW SOUTH WALES: Off Broadwater (18 fm). QUEENSLAND: Gulf of Carpentaria.

Distribution.—East coast of Africa, Gulf of Aden, coasts of India, Indonesia, Ceylon, Andaman Is.

Discussion.—In view of the limited material (1 immature female from New South Wales and 1 immature male from the Gulf of Carpentaria) the author was unable to make detailed studies on distinguishing features of this species. To quote Schmitt (1926), "The distinction of true *Peneus indicus* from its near relatives and varietal forms is by no means satisfactory". It seems justified to add that the great variability of juveniles makes their study more complicated. Alcock's (1906) and Schmitt's characterization, using the discrepancy in length of the dactyl on the 3rd maxillipeds, is quite reliable for diagnostic studies. However, more detailed observations on adult and juvenile material are highly desirable in order to seek primary distinguishing features, which will clear up some remaining nomenclatural problems.

PENAEUS MERGUIENSIS De Man

Plate 1, Fig. 4; Plate 5, Fig. 4; Plate 8, Fig. 4

Penaeus merguiensis De Man, 1888, p. 287, pl. 18, fig. 8; pl. 19, fig. 1; 1911, p. 104, pl. 9, fig. 33*a*. Boone, 1935, p. 96, pl. 24, fig. 7. Barnard, 1950, p. 590.

Penaeus indicus var. *merguiensis* De Man, 1892, p. 511.

Peneus indicus var. *merguiensis* Alcock, 1906, p. 13, pl. 2.

Peneus merguiensis Schmitt, 1926, pp. 360, 361.

Vernacular name: banana prawn.

Rostral formula usually 7/4, range 6-8/3-4. Rostrum slightly curved, apex straight, extending to tip of antennal scale. The upper blade conspicuously high, assuming a triangular, laminate shape. Anterior dorsal rostral tooth invariably placed in advance of the terminal segment of antennular peduncle. Lateral grooves not quite reaching to gastric tooth. Postrostral carina feebly developed, bearing 1 or 2 flat-topped indications of depressions. Carapace smooth; subhepatic crest absent. Abdominal segments 4-6 distinctly carinated, keel on last segment ending acutely. Uropoda elongated, telson without lateral spines. A small but distinct non-setose exopodite on the 5th pair of pereiopoda. Dactyl of 3rd maxillipeds of adult male scarcely half as long as propodus.

Generally, the shape of the thelycum is much like that of *indicus*. The lateral plates, however, form together a more oval pad, and the anterior margin of the median plate is more rounded than in *indicus*.

The petasma is figured in Plate 5, Figure 4.

Length up to 220 mm (8½ in.).

Colour in life pale cream (body semi-translucent), speckled with brown, olive green or light green pigment spots. Crest of carapace and abdomen light brown, pereiopoda yellow. Uropoda coloured in a combination of yellow, green, and brownish shades, resembling a ripening banana. Antennae brown, not banded; antennulae spotted.

Material.—NEW SOUTH WALES: Off Tweed Heads, Byron Bay, Lennox Head, Ballina, Evans Head, and Yamba (6-25 fm). QUEENSLAND: Moreton Bay (6-8 fm), Mackay (Pioneer R.), Prudhoe I. (18 fm).

Distribution.—East and west coasts of Australia, N. of lat. 29° S., Mergui Archipelago, Indonesia, India, Philippines, New Guinea, New Caledonia.

Discussion.—De Man (1888) described this form as a distinct species, but regarded it later (1892) as a variety of *P. indicus*. The same author (1911) finally restored it to the status of a species.

P. merguiensis is one of Queensland's most important commercial species, occurring in the estuarine area and offshore. It has been recently captured off Bundaberg in considerable quantities, and it is sometimes abundant even in Moreton Bay.

This species, well known to fishermen as the "banana prawn", has not been previously considered abundant south of Cape Moreton in ocean waters. On some occasions it occurs, however, along the far north coast of New South Wales, and has been captured commercially during June-July 1954 as far south as off Yamba in 6-25 fm.

PENAEUS LATISULCATUS Kishinouye

Penaeus latisulcatus Kishinouye, 1900, p. 12, pl. 2, fig. 2; pl. 7, figs. 2, 2*a*. De Man, 1911, p. 108, pl. 9, figs. 35*a*, *b*. Pesta, 1915, p. 111, fig. 3. Anderson and Lindner, 1943, p. 307.

Peneus latisulcatus Alcock, 1906, p. 47. Schmitt, 1926, pp. 359, 365, 368. Hale, 1927, p. 38, fig. 30.

Vernacular names: king prawn, furrowed prawn.

Rostral formula 9-11/1, usually 10/1. Rostrum slightly curved, not exceeding terminal segment of antennular peduncle. Paralleling the distinctly sulcate postrostral carina there is 1 pair of lateral grooves, extending almost to the posterior margin of the carapace. In adults their width is greater than that of the postrostral median sulcus. Postocular crest forming a single loop. Accessory pair of lateral adrostral sulci absent. Carapace smooth; telson armed with 3 pairs of lateral spines.

The lateral plates of the thelycum are separated medially by a narrow but discernible fissure, their lateral margins are posteriorly distinctly diverging. The median plate bears anteriorly 2 knob- to horn-like protuberances, which vary in size and shape with growth.

The petasma has 2 short submedian protuberances, which are only slightly bent, and do not tend to overhang the distal margins of the side plates.

Length up to 195 mm (7½ in.).

Colour in life light brown to reddish. Crest on carapace and abdomen dark red, pereiopoda yellow to orange, antennal scales and uropoda reddish, the uropoda with violet to dark red tips. Antennae not banded. There are many ecomorphic alterations in the coloration of the body; the abdominal segments may show occasionally a faint "tiger" pattern of darker crossbands.

Material.—NEW SOUTH WALES: Sussex Inlet (3-4 fm), Greenwell Point (12-15 fm).

Distribution.—Northern Queensland, Western Australia, South Australia, Japan, Formosa, Indonesia, Red Sea.

Discussion.—This species has not yet been found on the central and north coast of New South Wales, but it has been recorded by Schmitt (1926) from Bowen, Qld., and Kangaroo Island, S.A., and by Hale (1927) from South Australia. In view of this rather wide distribution in Australian waters and of the apparently unfilled niche along the main coastline of New South Wales and Queensland, it seems very probable that *P. latisulcatus* may have the centre of its abundance along the west coast of Australia. Unfortunately the author has been unable to secure material from Western Australia to confirm this theory, and more detailed ecological studies are desirable.

PENAEUS PLEBEJUS Hess

Plate 2, Figs. 4-5; Plate 5, Fig. 3; Plate 8, Fig. 3

Penaeus plebejus Hess, 1865, p. 168, pl. 7, fig. 19. De Man, 1911, pp. 96, 108-11, pl. 9, fig. 36*a*. Pesta, 1915, p. 112, figs. 4, 5. Dakin, 1938, pp. 163-83, pl. 1-7 (life history); 1940, pp. 354-9, figs. 1-15 (embryology).

Penaeus canaliculatus Haswell, 1879, p. 38; 1882, p. 198 (non Olivier (1811)). Ogilby, 1893, p. 202 (non Olivier (1811)). Stead, 1898, p. 209 (non Olivier (1811)).

Penaeus canaliculatus var. *australiensis* Bate, 1888, p. 248, pl. 32, fig. 3.

Peneus plebejus Schmitt, 1926, pp. 367-70, pl. 65, figs. 1-4; pl. 68, fig. 1.

Vernacular name: king prawn.

Rostral formula usually 10/1. Rostrum slightly curved, not exceeding terminal segment of antennular peduncle. Paralleling the distinctly sulcate postrostral carina, there is 1 pair of lateral grooves, extending almost to the posterior margin of the carapace. In adults their width is greater than the width of the postrostral median sulcus. In addition to these grooves on either side of the rostrum, about midway between them and the crest of the teeth there is another groove, commencing near the base of the 1st tooth and continuing to the foremost tooth. Postocular crest forming a double loop, each of them being separated by deep but narrow incisions, the inner somewhat shorter than the outer. Carapace smooth; telson armed with 3 pairs of lateral spines.

The lateral plates of the thelycum meet medially for the posterior three-quarters of their length and are distinctly separated by a narrow fissure. Their lateral margins are more or less parallel throughout their length. The posterior part of the median plate is longer than in *latisulcatus*, and the protuberances on its anterior margin are usually not very prominent.

The petasma is very much like that of *latisulcatus.*

Length up to 205 mm (8 in.).

Colour in life greenish (semi-translucent) to light brown, pereiopoda light yellow, uropoda bright blue with red or orange fringe. Crest on carapace and abdomen dark brown, antennae yellow, not banded. As in *latisulcatus,* there is a great variation in the coloration of the body of *plebejus.* The pleonic segments, for example, of specimens taken in Sydney Harbour are almost invariably banded with darker crossbands.

Material.—NEW SOUTH WALES: Along the whole coastline, somewhat more abundant in perifluvial areas. QUEENSLAND: South coast, including Moreton Bay, Mackay (Pioneer R.), and Repulse Bay.

Distribution.—New South Wales, Queensland, Victoria, New Zealand.

Discussion.—*P. plebejus,* together with *Metapenaeus macleayi* in New South Wales and *P. merguiensis* in Queensland, is a commercial species of great importance. Well known to estuarine and offshore fishermen as the king prawn, this species is abundant along the whole coastline of New South Wales and the southern half of Queensland and has been reported to the author by fishermen even from Victoria. Its optimal habitat in adult life is offshore in about 15-25 fm, but it has also been captured by the author with experimental baited traps, together with *carinatus* and *esculentus,* in depths to 75 fm. It is somewhat more abundant in perifluvial areas, and juvenile stages are found in tidal rivers, lagoons, and even in landlocked coastal lakes. Juveniles are associated in estuarine areas invariably, and in the inner littoral areas often, with *Metapenaeus macleayi.* Trapping tests in the outer littoral area proved its co-appearance with *esculentus,* although it has not yet been captured commercially beyond the 25 fm line.

Dakin (1938, 1940) and Dakin and Colefax (1940) made valuable contributions towards the knowledge of the embryology of this species.

PENAEUS MACCULLOCHI Schmitt

Peneus maccullochi Schmitt, 1926, pp. 359, 370-1, pl. 66, figs. 1-3.

Rostral formula 10/1 (11/1 in Schmitt's holotype). Rostrum slightly curved, not exceeding terminal segment of antennular peduncle. Postrostral sulcus and accessory adrostral grooves as in *plebejus.* The lateral grooves, paralleling the comparatively short median sulcus, fuse behind the postrostral carina, forming an X-shaped depression. Postocular crest forming a double loop (as in *plebejus*), but the separating narrow incisions seem almost equal in length. Carapace smooth; telson armed with 3 pairs of lateral spines.

The petasma of the single male bears no characters distinctive from *plebejus.*

Length of captured specimen 110 mm ($4\frac{1}{2}$ in.).

The colour in life of this species has not been observed.

Material.—NEW SOUTH WALES: 1 male, 1 mile off Broadwater beach, 18 fm.

Distribution.—1 male previously found off North Reef, Qld., in about 70 fm during the cruise of F.I.S. *Endeavour.*

Discussion.—As far as is known to the author, this species has been found for the first time since it was taken originally by the *Endeavour* and described by Schmitt (1926). Unfortunately only 1 damaged and immature male specimen was secured during the present investigations. It is, however, quite possible that this species could have been previously overlooked, owing to its similarity in general structure to *plebejus.* Further detailed morphological and ecological studies are desirable to permit the observation of distinguishing criteria, particularly of females.

KEY TO INDO-PACIFIC GENERA OF THE PARAPENAEUS GROUP

1. Longitudinal and transverse sutures present on carapace. Exopodites present in form of minute, hardly discernible rudiments on all legs. Telson armed with a subapical pair of fixed spines, preceded by 1 pair of mobile spinules. Petasma symmetrical .... genus *Parapenaeus* Smith
Longitudinal and transverse sutures absent on carapace. Exopodites distinctly present on all legs. Telson armed with a subapical pair of fixed spines, preceded by more than 1 pair of mobile spines (genus *Penaeopsis* Bate) 2
2(1). Petasma symmetrical ....
.... subgenus *Penaeopsis* Bate (sensu stricto, Burkenroad 1934*b*)
Petasma asymmetrical ....
.... subgenus *Metapenaeopsis* Bouvier (redefined, Burkenroad 1934*b*)

The three known species of *Parapenaeus* occurring in the Indo-Pacific region, *longipes* Alcock, *investigatoris* Alcock & Anderson, and *fissurus* Bate, have been keyed out by Anderson and Lindner (1943). As they have not yet been recorded from Australian waters their definition is here omitted.

The genus *Penaeopsis* Bate, as restricted by Burkenroad (1934*b*), has been divided into two subgenera, mainly on account of the shape of the petasma. The two species of the first (*Penaeopsis* Bate s.s.) known from the Indo-Pacific region, *serratus* Bate and *rectacutus* Bate, have not yet been recorded from Australian waters, and seem not to be satisfactorily separated. Burkenroad's second subgenus (*Metapenaeopsis* Bouvier rdf.) comprises a considerable number of often confused species, of which one, *novae-guineae* (Haswell), occurs with certainty in Australia.

Since Schmitt (1926) identified one of Haswell's "*Penaeus Palmensis*" from the Macleay Museum in Sydney (collected off Darnley I., Torres Strait) as *Penaeopsis mogiensis* Rathbun (1902, 1903), it is possible that even this species may occur in Australian waters. During the present investigations, however, it has not been found.

Genus PENAEOPSIS Bate

PENAEOPSIS (METAPENAEOPSIS) NOVAE-GUINEAE (Haswell)

Plate 4, Fig. 4; Plate 7, Figs. 1, 2

Penaeus Novae-Guineae Haswell, 1879, p. 43; 1882, p. 203. Alcock, 1906, p. 55. Schmitt, 1926, p. 341.

Penaeus Palmensis Haswell, 1879, p. 43; 1882, p. 204. Schmitt, 1926, p. 344.

Metapeneus palmensis Alcock, 1906, p. 51.

Metapeneus stridulans Alcock, 1906, p. 27, pl. 5, figs. 14-14*d*.

Penaeopsis palmensis De Man, 1911, pp. 8, 55, 73.

Penaeopsis stridulans De Man, 1911, p. 65, pl. 7, figs. 20*a*, *b*. Pesta, 1915, p. 104.

Penaeopsis novae-guineae Schmitt, 1926, p. 338, pl. 61, figs. 1, 2*a*, *b;* pl. 68, figs. 2*a*, *b*. Hale, 1927, p. 39, fig. 31.

Rostrum somewhat elevated, the tip uptilted, sometimes reaching to terminal segment of antennular peduncle, but often shorter, armed dorsally with 4-8 teeth. The epigastric tooth small, often blunt and isolated. Postrostral crest absent. Antennal spine very prominent, hepatic spine pronounced but small. Antero-inferior angle of carapace with branchiostegal spine. In both sexes there is a pair of stridulating organs situated on each side of the carapace, near the middle of the posterior end of the branchiostegite. Each organ is composed of 5-15 ridges on a slightly raised, non-pubescent, straight or curved band. The number of ridges and the shape of their arrangement vary greatly, the organ being usually better developed in females than in males. Carapace and abdomen thickly tomentose.

The 2nd abdominal tergum is medially carinated for less than its posterior half, the 3rd in almost all its extent; the carina in both segments is sulcate. The 4th to 6th abdominal terga are sharply carinated. The 6th abdominal somite is about twice as long as the 5th, but shorter than the telson, which bears 3 pairs of lateral mobile spines in addition to the fixed subapical pair.

The thelycum is quite complex and is shown in Plate 7, Figure 1.

The petasma is asymmetrical, the distolateral projection of the left petasmal endopod being larger than the right one, and ending in a crown of stiff filaments.

Length of large females 95 mm (3¾ in.), of males 75 mm (3 in.).

Colour in life tan to reddish, with purplish cloudings and blotches, appendages pink to orange. The coloration of this species varies greatly with the environment; specimens taken in Sydney (Middle Harbour) are usually bright red.

Material.—NEW SOUTH WALES: Tweed Heads, Byron Bay, Lennox Head, Ballina, Evans Head, Yamba (15-25 fm); Sydney Harbour (3-6 fm). QUEENSLAND: Southport (12 fm), Moreton Bay (6-8 fm).

Distribution.—Western Australia, Queensland, New South Wales, Hongkong, Japan, India, Indonesia, New Guinea, Red Sea, Suez.

Discussion.—This rather widely distributed species shows extraordinary variability in the toothing and shape of the rostrum, the more or less distinct development of the branchiostegal spine, the form of the stridulating organ, and the number of its ridges. Haswell (1879, 1882) regarded these differences as sufficient to create 2 separate species, his *Penaeus Novae-Guineae* and *Penaeus Palmensis.* Alcock (1906) listed both of these species as doubtful forms on the ground of Haswell's insufficient and partly incorrect descriptions. He himself described Indian specimens under the name of *Metapeneus stridulans* and presented excellent definitions and illustrations. Later De Man (1911), following a survey of the *Siboga* material, changed its generic name to *Penaeopsis* and came to the conclusion that all specimens with stridulating organs should be referred to the same species. Schmitt (1926) restored the precedence and raised Haswell's *Novae-Guineae* from a doubtful systematic position to a proper species. Consequently, Alcock's *Metapeneus stridulans* (= De Man's *Penaeopsis stridulans*), in spite of being a well-known species, became relegated to the position of a synonym. In view of Burkenroad's (1934*b*) revisions, this species is to be regarded as belonging to the subgenus *Metapenaeopsis* Bouvier (rdf.).

P. (*M.*) *novae-guineae,* because of its small size, is not regarded in New South Wales as a commercial species, although it occurs sporadically in large schools. Its habitat is not necessarily perifluvial, but its influx into the estuarine area during December and January is considerable. It is often confused with *Trachypeneus* (*Trachysalambria*) *curvirostris* (Stimpson), and is invariably associated with this species. In view of its wide distribution and its being recorded by Hale (1927) even from South Australia, it may probably occur all around Australia.

KEY TO AUSTRALIAN AND INDO-PACIFIC GENERA OF THE TRACHYPENEUS GROUP

1. Carapace without longitudinal and transverse sutures 2
Carapace with longitudinal or transverse sutures or both 3

2(1). Pleurobranch present on somite 13; exopodites absent from 5th pair of pereiopoda ....*Metapenaeus* Wood-Mason & Alcock
Pleurobranch absent on somite 13; exopodites on all of the pereiopoda ....*Trachypeneopsis* Burkenroad

3(1). Antennal spine without buttress at its base; spine on basis of 3rd pereiopoda. Transverse suture on carapace present ....*Atypopeneus* Alcock
Antennal spine with buttress on its base. Spine absent from basis of 3rd pereiopoda (except in female of *Parapeneopsis maxillipedo*) 4

4(3). Epipodites absent from 3rd pereiopoda ....*Parapeneopsis* Alcock
Epipodites present on 3rd pereiopoda ....*Trachypeneus* Alcock

Genus METAPENAEUS Wood-Mason & Alcock

KEY TO EASTERN AUSTRALIAN SPECIES OF THE GENUS METAPENAEUS WOOD-MASON & ALCOCK

1. Telson armed with prominent mobile lateral spines 2
Telson without prominent spines, but with numerous minute mobile spinules ...3

2(1). Carapace more or less glabrous, pubescence only in sulci of carapace. Coxae of 4th pereiopoda in adult female produced into prominent quadrangular plates. Postrostral carina not reaching to posterior margin of carapace. Telson armed with 4 pairs of lateral spines ....*M. macleayi* (Haswell)

Carapace and abdomen covered with dense pubescence, arranged in irregularly triangular patches. Coxae of 4th pereiopoda of adult female produced into prominent blunt spines. Postrostral carina reaching almost to posterior margin of carapace. Telson armed with 3 pairs of lateral spines ....*M. endeavouri* (Schmitt)

3(1). Posthepatic ridge prominent throughout its length. 1st pair of pereiopoda bispinose. Lateral plates of adult thelycum bowl-like concave, posteromedially almost fused. Distomedial projections of adult petasma more prominent than distolateral ....*M. incisipes* (Bate)

Posthepatic ridge obscure and only partially (posteriorly) developed. 1st pair of pereiopoda unispinose. Lateral plates of adult thelycum slightly convex, somewhat retort-shaped, posteromedially distinctly separated. Distolateral projections of adult petasma more prominent than distomedial ....*M. mastersii* (Haswell)

METAPENAEUS MACLEAYI (Haswell)

Plate 3, Fig. 1; Plate 7, Fig. 3; Plate 9, Fig. 1

Penaeus macleayi Haswell, 1879, p. 40; 1882, p. 210. Ogilby, 1893, p. 204. Phillipps, 1925, p. 3, pl. 2, fig. 1.

Metapeneus macleayi Alcock, 1906, pp. 17, 50.

Penaeus haswelli Phillipps, 1925, p. 3.

Penaeopsis macleayi Schmitt, 1926, p. 333, pl. 60, figs. 1-5. Boone, 1935, p. 75, pl. 19, fig. 3. Dakin, 1938, p. 166.

Vernacular name: school prawn.

Rostrum dorsally armed with 5-7 (usually 6) teeth, including the epigastric tooth, and reaching to tip of antennal scale. Its distal quarter is toothless, styliform, and distinctly uptilted. The postrostral carina is broad and low, and disappears before reaching the posterior third of the carapace. The sulci of the carapace carry more or less pubescence, otherwise the carapace and abdomen are glabrous. Orbital margin dentiform. Hepatic spine about as strong as antennal spine. The 4th pleonic tergum is only slightly carinated, whilst the terga of the 5th and 6th abdominal segments are distinctly so. The telson is armed with 4 pairs of unequally spaced mobile spines, of which the subterminal pair is the most prominent.

All 3 pairs of chelipeds are armed with a spine on the basis. In the adult male the last pair of pereiopoda has the proximal end of the merus notched on its outer side. This notch is deepened anteriorly by a triangulate tooth.

The petasma is symmetrical, its 2 rigid segments tightly folded and interlocked to form a compressed tube; it is figured in Plate 7, Figure 3.

The thelycum is characteristic and complex, and is shown in Plate 9, Figure 1.

Length up to 153 mm (6 in.).

Colour in life greenish translucent with numerous brown or olive green pigment spots. Tips of uropoda blue-green to violet, pereiopoda and pleopoda yellow.

Material.—Very abundant in estuaries and perifluvial areas of the inner littoral zone. Along the whole coastline of New South Wales and southern Queensland up to Cape Moreton. Apparently not occurring in Moreton Bay itself.

Distribution.—New South Wales, adjacent Victorian waters, New Caledonia (Boone 1935).

Discussion.—This is the most important commercial species of the New South Wales prawn industry, and is captured in estuarine areas as well as in offshore waters. Well known to fishermen as "school prawn" because of its extensive schooling habits, this species appears sporadically and in large schools in perifluvial areas, chiefly shortly after river floods. The school prawn usually enters the offshore commercial catch in the middle of December, and shows peak productions between March and May. Its optimal habitat in adult life is situated offshore in about 12-20 fm; its juvenile stages are found in tidal rivers, in lagoons, and even in temporarily landlocked lakes. It is interesting to note that the largest females, often exceeding 6 in. in length, are invariably captured between April and June off Lennox Head, north of Ballina (N.S.W.) in about 18 fm.

METAPENAEUS ENDEAVOURI (Schmitt)

Plate 3, Fig. 2; Plate 6, Fig. 5; Plate 9, Fig. 2

Penaeopsis endeavouri Schmitt, 1926, p. 329, pl. 59, figs. 1-3; pl. 68, fig. 4.
Metapenaeus endeavouri Burkenroad, 1934*b*, p. 37.

Vernacular name: Endeavour prawn.

Rostrum armed with 10-12 (usually 10) teeth, including the epigastric tooth. It is somewhat ascending and extends as far as, or slightly beyond the distal border of the 2nd joint of the antennular peduncle. Its apex is slightly uptilted, somewhat more in females than in males. The postrostral carina is distinct, and reaches almost to the posterior margin of the carapace. The pubescence on carapace and abdomen is very prominent. On the carapace, the pubescence occupies the whole dorsum and the greater part of the branchial region. Likewise all abdominal epimera are covered with pubescence, which appears to be arranged in irregularly triangular patches. The 2 pubescent patches on the epimeron of the 1st abdominal segment are each more than twice as wide as the interval between them. Orbital (postocular) tooth only a blunt angle. The 4th pleonic tergum is carinated only on its posterior half, the terga of the 5th and 6th abdominal segments throughout their length. The carina on the 6th somite ends posteriorly in a tooth. Posthepatic carina on carapace undiscernible. Telson armed with 3 pairs of lateral mobile spines.

Petasma bearing anterolateral prominent spines. It is figured in Plate 6, Figure 5.

The median plate of the thelycum is slightly emarginate in the middle of the anterior margin; the lateral plates are evenly rounded. The coxae of the 4th pair of pereiopoda are produced into prominent, blunt spines, somewhat overhanging the lateral plates of the thelycum.

Length up to 160 mm (6¼ in.).

Colour in life light brown to pinkish, appendages pink or yellow, tips of uropoda bluish violet.

Material.—NEW SOUTH WALES: Tweed Heads, Byron Bay, Ballina, Yamba (12-18 fm). QUEENSLAND: Moreton Bay (6-8 fm).

Distribution.—Recorded previously by Schmitt (1926) from Pine Peak, and southern Queensland coast. Recently recorded from Shark Bay, W.A.

Discussion.—*M. endeavouri* appears to be very closely related to *intermedius* Kishinouye (1900), and to some extent even to *monoceros ensis* de Haan (1850), which latter 2 species the author has not seen. Although Schmitt separated his *endeavouri* satisfactorily, more detailed comparative observations are desired for a future general review of all *Metapenaei.*

This species does not play a big part in prawn production, either in Queensland or in New South Wales. It seems to have the same ecological boundaries as *Penaeus merguiensis,* the banana prawn, but with a sharp southern boundary somewhere around Stradbroke I., and it occurs only occasionally further south. Stray specimens have been found as far south as Yamba.

METAPENAEUS INCISIPES (Bate)

Plate 3, Fig. 3; Plate 6, Figs. 3, 4; Plate 9, Fig. 4

Penaeus incisipes Bate, 1888, p. 257, pl. 24, fig. 2. Kishinouye, 1900, p. 18, pl. 4, fig. 2; pl. 7, fig. 6.
Metapeneus incisipes Alcock, 1906, p. 51.
? *Penaeopsis monoceros* Schmitt, 1926, p. 325 (not synonymy nor plate).
? *Penaeus incisipes* Blanco and Arriola, 1937, p. 223, pl. 2, fig. 5.

Vernacular names: greasy-back, offshore greasy-back.

Rostrum dorsally armed with 8-10 (usually 9) teeth, including the epigastric tooth. It is quite low and slightly sigmoid in mature males, and somewhat higher in mature females, where the apex appears to be slightly uptilted. In males the middle rib of the rostrum emerges from the carapace horizontally and continues slightly downwards to the foremost rostral tooth, where it regains its horizontal position. In both sexes the rostrum slightly exceeds the anterior margin of the terminal segment of the antennular peduncle. The postrostral carina is quite pronounced and reaches almost to the posterior margin of the carapace. The posthepatic carina is very prominent and extends from the hepatic spine almost to the posterior margin of the carapace, thus defining a pronounced boundary of the branchial region. The pubescence on carapace and abdomen is quite prominent. It occupies almost the whole dorsum of the carapace, about a third of the branchial region, and in irregular setose patches the terga and epimera of the pleonic somites. The rounded marginal area between the orbital denticle and the rostrum is distinctly pubescent. The anterior half of the sternum of the 6th abdominal segment bears 2 sublateral, longitudinal narrow patches of pubescence. The ellipsoid, streamlined elevation on the posterior third of the same sternum is anteriorly framed by several transverse rows of setae. Postocular (orbital) tooth distinctly dentiform. Peduncles of pleopoda thickly setose. The 2nd pleonic segment bears dorsally an elongate tubercle, the 3rd is carinated in its posterior half, and the last 3 abdominal segments are sharply carinated, the carina on the 6th ending in a short tooth. The 1st pair of chelipeds armed with a spine on basis and ischium, the latter being small, but pronounced. Telson armed with numerous hardly discernible minute mobile spinules.

The lateral plates of the mature thelycum are concave, and postero-medially almost fused; their lateral margins are considerably elevated and form crescent-shaped ridges. The median plate of the thelycum is narrow, laterally compressed, and medially grooved. Its lateral margins are parallel almost throughout their length.

The characteristic petasma is figured in Plate 6, Figures 3 and 4.

Length up to 140 mm ($5\frac{1}{2}$ in.).

Colour in life light tan to brown, pleopoda, uropoda, and antennae red. Peduncles of pleopoda and tips of uropoda purple. Ischia and mera of pereiopoda distinctly "striped" with orange (or red) and cream (or yellow).

Material.—NEW SOUTH WALES: Byron Bay, Lennox Head, Ballina, Broadwater, Evans Head, Stockton Bight, Greenwell Point (12-18 fm). QUEENSLAND: Moreton Bay (6-8 fm), Prudhoe I. (25 fm).

Distribution.—Owing to the confusion of this species with *M. monoceros* Fabricius, its actual distribution is difficult to ascertain; as *Penaeus incisipes,* it is recorded from the Philippines by Bate and from Japan by Kishinouye.

Discussion.—The problem of a satisfactory and positive identification of most of the species of *Metapenaeus* with minute mobile spinules as telson armature will remain an extremely difficult one unless comprehensive morphological, ecological, and comparative studies are carried out by a body of closely cooperating specialists throughout the Indo-Pacific region. It would seem particularly unwise to create possible new species prior to such a review and to run the risk of adding to the already existing synonymy.

According to Burkenroad (in Morris and Bennett 1951), who carried out detailed but as yet unpublished studies on species of the *monoceros* group, India is the eastern ecological boundary for *M. monoceros* Fabricius. Earlier workers on Australian species, including Schmitt, however, described offshore forms of this group as *monoceros*, without giving details "of this rather widely distributed species". Thus it happened that another typical Australian species, although showing marked morphological and ecological differences, was lumped under this name by more recent Australian writers. This estuarine species, well known to fishermen as greasy-back or greentail, occurs in some coastal lakes of New South Wales and in Moreton Bay, Qld., and has been recorded also from Western Australia. It is dealt with below as *M. mastersii.*

Bate's (1888) description and figures are less accurate than Kishinouye's (1900), but both their drawings of the petasma agree well with this species (*incisipes*), as found during the present investigations, and differ from *monoceros* Fabricius in many regards. However, Bate's figure of the thelycum either refers to another genus, perhaps *Parapeneopsis* as Burkenroad (1934*b*, p. 29) suggests, or it is a misrepresentation by the artist. Alcock (1906) considered Bate's species a doubtful one, thus aiding its relegation to the position of a synonym of *monoceros* by later writers. The author has not seen Bate's type specimen, but the New South Wales specimens seem to differ slightly from his description; however, they are identical with *incisipes* Kishinouye (1900). In comparison with mature Indian specimens of *monoceros,* the apical convoluted flaps of the adult petasma of *incisipes* are parallel, high, and very prominent. The lateral plates of the adult thelycum of *incisipes* are much wider than those of *monoceros,* their inner margins are less regularly defined, and their position is more transverse than in *monoceros.* A series of 4 adult males and 12 adult females show no variations in the shape and structure of their genitalia, and are quite different from those of adult Indian *monoceros.*

One adult female, collected in Moreton Bay, differs from this species by the form and structure of its thelycum and by its vivid pink coloration. The lateral plates are almost fused, forming a deep bowl covered with setae. Unless more specimens, particularly males, are found, its separation cannot be attempted.

M. incisipes appears to be in New South Wales a strictly offshore species, and has been only rarely found in the "inside" area. It occurs, however, with *M. mastersii* in Moreton Bay. Although occasionally abundant off the far north coast of New South Wales, it has not yet been captured there in commercial quantities.

METAPENAEUS MASTERSII (Haswell)

Plate 3, Fig. 4; Plate 4, Fig. 1; Plate 6, Figs. 1, 2; Plate 9, Fig. 3

Penaeus Mastersii Haswell, 1879, p. 42; 1882, p. 203. Schmitt, 1926, p. 327, pl. 58, figs. 1, 2.

Penaeus sp. Whitelegge, in Ogilby 1893, p. 203.

Penaeopsis monoceros Schmitt, 1926 (part), p. 325, pl. 58, figs. 1, 2. Dakin, 1938, p. 166.

"Dana" Metapenaeus, sp. nov.; Morris and Bennett, 1951, p. 164, pl. 12, figs. 1-96.

Vernacular names: greasy-back, greentail.

Rostrum more or less straight, distinctly ascending, exceeding distal margin of the 2nd joint of the antennular peduncle. Rostral teeth usually 9, the foremost tooth usually separated by a wider interval from the penultimate. Postrostral carina broad and faint, not reaching to the posterior margin of the carapace. Posthepatic carina only partially developed, discernible only along the posterior quarter of the carapace. Pubescence present in irregular grooves on dorsum of carapace, branchial region more or less glabrous. The rounded area between postocular tooth and rostrum naked. Peduncles of pleopods with narrow setose grooves. The sternal ellipsoid elevation on the 6th pleonic somite not preceded by transverse rows of setae; however, on the anterior third of this sternum 1 pair of sublateral longitudinal rows of sparse setae may be present. The first 3 pairs of pereiopoda armed with a spine on the basis, the inner apex of the ischium of the 1st pereiopoda forming not more than a blunt prominence. In adult males the merus of the 5th pereiopoda bears a notch and a spine. Telson armed with numerous minute mobile spinules.

The lateral plates of the thelycum are convex, somewhat transverse, and posteromedially not fused. They are retort- or kidney-shaped (Plate 9, Fig. 3). The median grooved plate is narrowest at the middle of its length, expanding about equally posteriorly and anteriorly. Its anterior margin has a rounded triangular shape and bears 3 characteristic tubercles. The coxae of the 4th pair of pereiopoda are produced into prominent semi-spherical plates.

The adult petasma is figured in Plate 6, Figures 1 and 2.

Mature females reach a total length of about 120 mm (4½ in.); mature males are always considerably smaller. In Lake Innes, N.S.W., this species seldom grows larger than 3¾ in.

Colour in life semi-translucent pale green, with numerous brownish green pigment spots. The tips and outer margins of the uropoda are rich green.

Material.—This typical Australian estuarine species is found in New South Wales chiefly in Lake Innes, Cathie Creek, the Tuggerah Lakes, and Lake Illawarra, but its occurrence is somewhat irregular. It is abundant also in Moreton Bay, Qld.

Distribution.—*M. mastersii* has been recorded previously from estuarine waters along the east, north, and west coasts of Australia.

Discussion.—The nomenclature of this species has been a problem, and hitherto this well-known and typical Australian form has had nothing more than a provisional name. It is even difficult to ascertain how often it may have been confused with other species under the name of *Metapenaeus monoceros* Fabricius, although possessing strikingly different characters from the latter. As this species is, apart from the Indian *M. dobsoni* Miers (Menon 1951), apparently the only penaeid which prefers estuarine waters of lower salinity (Dakin 1946), and even breeds there (Morris and Bennett 1951), it is quite understandable that it should have been overlooked by various expeditions and collectors working chiefly in ocean waters. However, owing to the estuarine character of prawning activities prior to 1947, its production, particularly in Tuggerah Lakes and Lake Illawarra, has been occasionally plentiful. Yet although this species became well known to fishermen it was disregarded by scientists.

Owing to the somewhat insufficient description by Haswell (1879, 1882), Alcock (1906) considered this species a doubtful one. Later writers regarded it as an immature *M. monoceros*, explaining some obvious differences by existing variations within this species. Whitelegge (in Ogilby 1893), although not associating Haswell's species with his *Penaeus* sp., appears to have been the first to draw attention to this "probably undescribed form, abundant at certain seasons in the Sydney market". However, his description is not sufficient to be of any value.

Schmitt (1926), although admitting some differences in the shape of the immature genitalia of *Penaeus Mastersii*, which was collected and identified by McCulloch and deposited in the Australian Museum, Sydney, surprisingly considered Haswell's separation of *Mastersii* unsubstantial, and placed this species within the limits of variations in *monoceros*. He had no hesitation in relegating Haswell's species, and even Whitelegge's *Penaeus* sp., to the position of a synonym of *monoceros*. Thus the trace of taxonomic evidence of the estuarine greasy-back became lost, and later Australian writers, studying this then important commercial species, recorded it as *Penaeopsis monoceros* and later as *Metapenaeus monoceros*. In the late twenties, scientists on the Danish research vessel *Dana* on a visit to Australia secured samples from the Sydney Fish Market and later handed their collection to Burkenroad. He, realizing the clear discrepancy with *monoceros*, proposed the provisional name *"Dana" Metapenaeus*, sp. nov.; however, a description of this new species has not been published since. Morris and Bennett (1951) were thus forced to publish important embryological studies under this provisional name, following the identification of samples by Burkenroad.

To avoid further nomenclatural confusion, the author has examined Haswell's cotype in the Macleay Museum at the University of Sydney. It has all the typical features of the discussed species: there is no evident spine on the ischium of the 1st pereiopoda; the postrostral carina does not reach to the posterior margin of the carapace; the posthepatic carina is faint and only partially developed; only the last 3 pleonic terga are carinated; the pubescence is not conspicuous, and is restricted mainly to the dorsum; the rounded marginal area between rostrum and orbital tooth is naked; and there are no rows of setae on the sternum of the 6th pleonic somite. This cotype unfortunately is too much damaged for the shape of its petasma to be of diagnostic value.

In conjunction with Mr. W. Dall (Department of Zoology, University of Queensland) the author has also examined 3 immature specimens from the Australian Museum, collected by McCulloch and identified by him as *Penaeus mastersii.* They are definitely identical with material collected during the present investigations. In view of the wide distribution of this species around Australia, and the thorough examination of all *Metapenaei* occurring along the north and east coasts of Australia by Dall (unpublished data), the identity of Haswell's *Penaeus Mastersii* with the discussed species appears to be satisfactorily proved. Haswell's (1879, 1882) name therefore takes precedence.

Owing to the irregular appearance of this species, and to the expansion of the offshore prawning activities, its commercial importance in New South Wales has decreased. Its State-wide unattractive vernacular name greasy-back should be dropped, and replaced by the more characteristic term greentail, more often used in Queensland.

Genus TRACHYPENEUS Alcock

The genus *Trachypeneus* has been subdivided by Burkenroad (1934*b*) on the ground of the presence or absence of epipodites on the first two pairs of pereiopoda into two subgenera *Trachysalambria* and *Trachypeneus.* During the present investigations *Trachypeneus* (*Trachysalambria*) *curvirostris* (Stimpson), apparently the only Indo-Pacific species of the first subgenus, has been found abundant in commercial offshore catches. *Trachypeneus* (*Trachypeneus*) *anchoralis* (Bate), a species belonging to the second subgenus, has been found off the far north coast of New South Wales, but seems to be very rare in this State.

TRACHYPENEUS (TRACHYSALAMBRIA) CURVIROSTRIS (Stimpson)

Plate 4, Figs. 2, 3; Plate 7, Figs. 4, 5

Penaeus curvirostris Stimpson, 1860, p. 44. Miers, 1878, p. 307. Kishinouye, 1900, p. 23, pl. 6, fig. 4; pl. 7, fig. 10.

Penaeus granulosus Miers, 1884, p. 295 (non Haswell (1879, 1882)).

Trachypeneus curvirostris Alcock, 1905, p. 523; 1906, p. 53. Schmitt, 1926, p. 353 (and synonymy), pl. 63, fig. 3.

Trachypeneus asper Alcock, 1906, p. 43, pl. 9, fig. 28.

Trachypenaeus anchoralis De Man, 1911, p. 88, pl. 8, fig. 28 (non Bate (1888)).

Trachypeneus (*Trachysalambria*) *curvirostris* Burkenroad, 1934*b*, p. 49. Anderson and Lindner, 1943, p. 314.

Rostrum distinctly uptilted in females, reaching to anterior margin of the 2nd joint of the antennular peduncle, often shorter. In males the rostrum is slightly uptilted and considerably shorter. Rostral teeth, including the epigastric tooth, usually 8. Postrostral carina present but faint. Branchiostegal spine absent, but antero-inferior angle somewhat pointed. Longitudinal suture on carapace just discernible, and not reaching posterior to the hepatic spine. The 2nd pleonic tergum bears an elongated tubercle, the 3rd to 6th pleonic terga are distinctly carinated. Carapace and abdomen are thickly tomentose. Epipodites present on 1st 2 pairs of pereiopoda, which are armed on the basis with a spine. The telson is armed with a subapical, readily discernible pair of lateral spines, and in advance of them with 1-3 pairs of minute, scarcely perceptible spines, often not more prominent than a blunt elevation. The armature of the telson shows a considerable variation.

The lateral plates of the thelycum are convex and medially fused. The cordiform median plate is longitudinally grooved and granulated (Plate 7, Fig. 4).

The petasma is figured in Plate 7, Figure 5.

Mature females occasionally reach a total length of about 120 mm (4½ in.), but are usually smaller. Mature males seldom grow larger than 3¼ in.

Colour in life usually pink to dull red, sometimes brown, uropoda with longitudinal red and white stripes.

Material.—This species is abundant in New South Wales from Tweed Heads to Wollongong; its occurrence further south is somewhat scarce. In southern Queensland it has been taken in Moreton Bay.

Distribution.—Japan, Formosa, Indonesia, Papua, Andaman Is., India, Persian Gulf, Red Sea, Port Darwin, Cape Jaubert (W.A.).

Discussion.—This well-known species, owing to its small size, is not considered of commercial value. It appears quite frequently in New South Wales in company with *Penaeopsis* (*Metapenaeopsis*) *novae-guineae*, occurring often sporadically during December-February.

TRACHYPENEUS (TRACHYPENEUS) ANCHORALIS (Bate)

Penaeus anchoralis Bate, 1888 (part), p. 258, pl. 35, fig. 1.
Trachypeneus anchoralis Schmitt, 1926, p. 348, pl. 62, figs. 1-3; pl. 68, fig. 3.
Trachypeneus (*Trachypeneus*) *anchoralis* Burkenroad, 1934*b*, p. 49.

Rostrum distinctly uptilted, reaching almost to anterior margin of the 2nd joint of the antennular peduncle. Rostral teeth, including the epigastric tooth, usually 9. Postrostral carina as in *T.* (*T.*) *curvirostris*. Antero-inferior angle of carapace not pointed as in *curvirostris*, but longitudinal suture as in *curvirostris*. The 2nd pleonic tergum bears a medially compressed tubercle, the 3rd to 6th pleonic terga are distinctly carinated. Carapace and abdomen are thickly tomentose. Epipodites are absent from the 1st 2 pairs of pereiopoda, present only on the 3rd. A basal spine is present on the 1st 2 pairs of pereiopoda as in *curvirostris*. The telson is armed with 3 pairs of hardly discernible spines, the subapical pair being the most prominent.

The thelycum is as figured by Bate and described by Schmitt. The median plate is cordiform and medially distinctly depressed. The transverse posterior plate has a rounded U-shape.

Colour in life deep brown to reddish brown.

Material.—2 females ex commercial catch 2 miles NE. of Evans Head, N.S.W. (18 fm).

Distribution.—Previously found in the Arafura Sea and off Bowen, Qld.

Discussion.—This species seems to inhabit only warmer seas, and is apparently extremely rare in New South Wales. More detailed observations, and particularly the capture of males, are highly desirable.

OTHER GENERA OF THE TRACHYPENEUS GROUP

Species of the genus *Parapeneopsis* Alcock have not yet been found off New South Wales. A description of those collected in warmer Queensland waters will be given in a forthcoming paper.

The genera *Trachypeneopsis* Burkenroad and *Atypopeneus* Alcock have not yet been recorded from Australia.

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EXPLANATION OF PLATES 1-9

PLATE 1

Fig. 1.—*Penaeus carinatus* Dana, male, 195 mm.
Fig. 2.—*Penaeus esculentus* Haswell, male, 175 mm.
Fig. 3.—*Penaeus caeruleus* Stebbing, male, 130 mm.
Fig. 4.—*Penaeus merguiensis* De Man, male, 180 mm.

PLATE 2

Fig. 1.—*P. carinatus*, carapace, lateral view.
Fig. 2.—*P. carinatus*, carapace, dorsal view.
Fig. 3.—*P. esculentus*, carapace, dorsal view.
Fig. 4.—*Penaeus plebejus* Hess, female, 185 mm.
Fig. 5.—*P. plebejus*, carapace, dorsal view.

PLATE 3

Fig. 1.—*Metapenaeus macleayi* (Haswell), female, 140 mm.
Fig. 2.—*Metapenaeus endeavouri* (Schmitt), female, 158 mm.
Fig. 3.—*Metapenaeus incisipes* (Bate), male, 140 mm.
Fig. 4.—*Metapenaeus mastersii* (Haswell), female, 112 mm.

PLATE 4

Fig. 1.—*M. mastersii*, total view.
Fig. 2.—*Trachypeneus* (*Trachysalambria*) *curvirostris* (Stimpson), female, 98 mm.
Fig. 3.—*T.* (*T.*) *curvirostris*, female, 98 mm.
Fig. 4.—*Penaeopsis* (*Metapenaeopsis*) *novae-guineae* (Haswell), female, 95 mm.

PLATE 5

Fig. 1.—Petasma of *P. carinatus.*
Fig. 2.—Petasma of *P. esculentus.*
Fig. 3.—Petasma of *P. plebejus.*
Fig. 4.—Petasma of *P. merguiensis.*

PLATE 6

Fig. 1.—Petasma of *M. mastersii*, ventral view.
Fig. 2.—Petasma of *M. mastersii*, dorsal view.
Fig. 3.—Petasma of *M. incisipes*, ventral view.
Fig. 4.—Petasma of *M. incisipes*, dorsal view.
Fig. 5.—Petasma of *M. endeavouri*, ventral view.

PLATE 7

Fig. 1.—Thelycum of *P.* (*M.*) *novae-guineae.*
Fig. 2.—Petasma of *P.* (*M.*) *novae-guineae*, ventral view.
Fig. 3.—Petasma of *M. macleayi*, ventral view.
Fig. 4.—Thelycum of *T.* (*T.*) *curvirostris.*
Fig. 5.—Petasma of *T.* (*T.*) *curvirostris*, ventral view.

PLATE 8

Fig. 1.—Thelycum of *P. carinatus.*
Fig. 2.—Thelycum of *P. esculentus.*
Fig. 3.—Thelycum of *P. plebejus.*
Fig. 4.—Thelycum of *P. merguiensis.*

PLATE 9

Fig. 1.—Thelycum of *M. macleayi.*
Fig. 2.—Thelycum of *M. endeavouri.*
Fig. 3.—Thelycum of *M. mastersii.*
Fig. 4.—Thelycum of *M. incisipes.*

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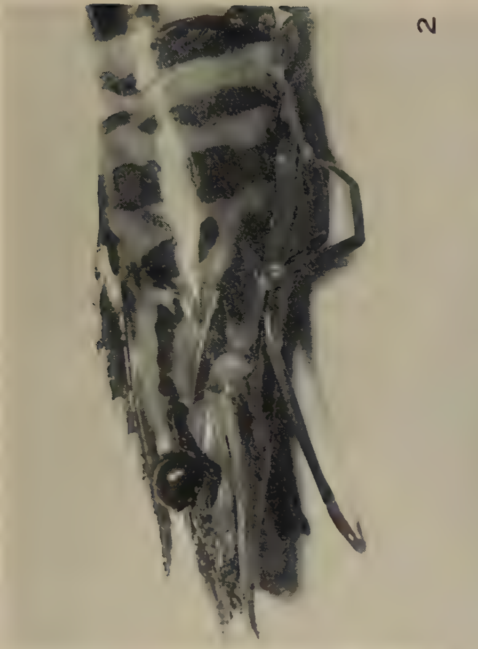

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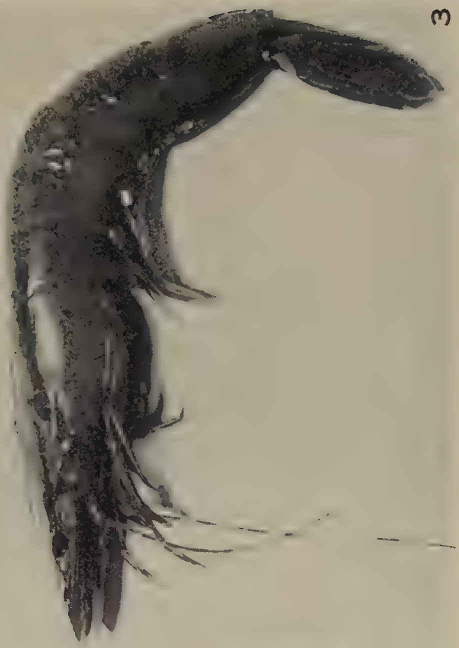

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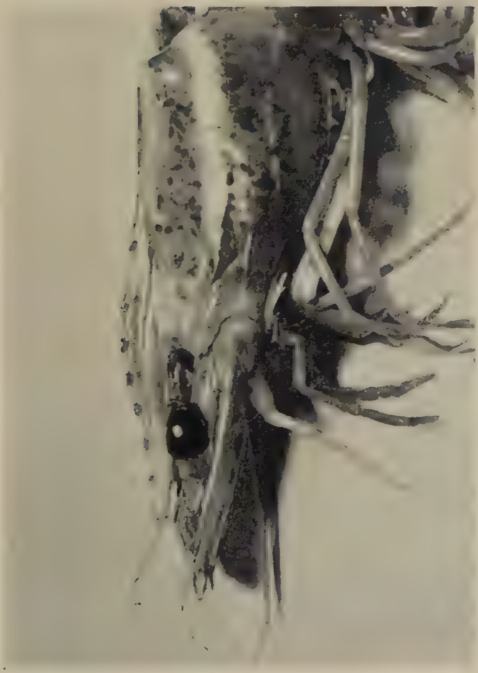

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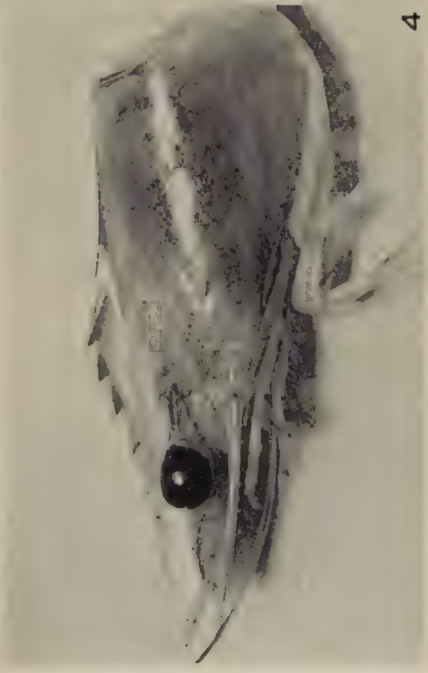

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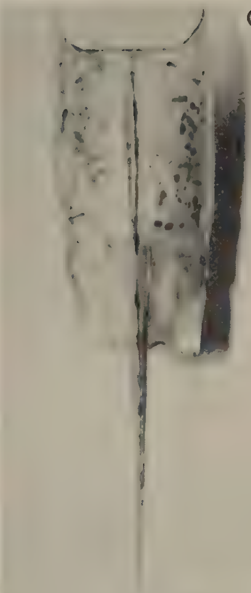
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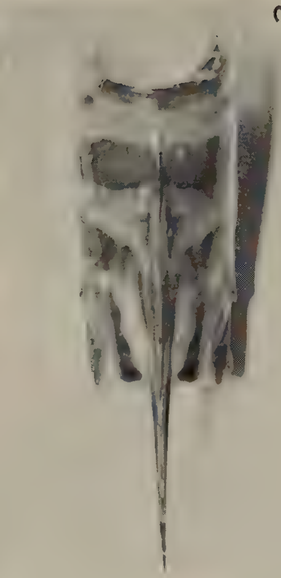
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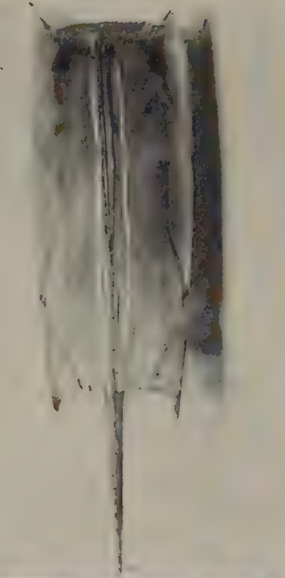
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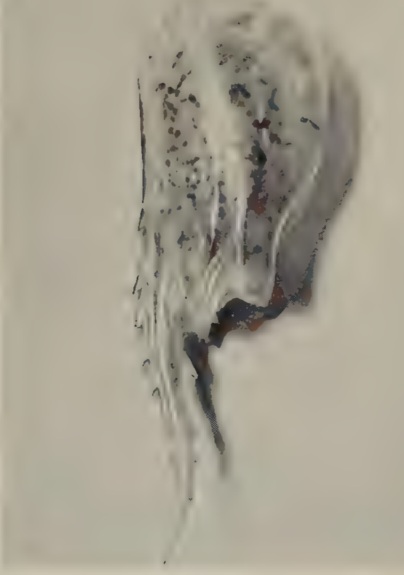
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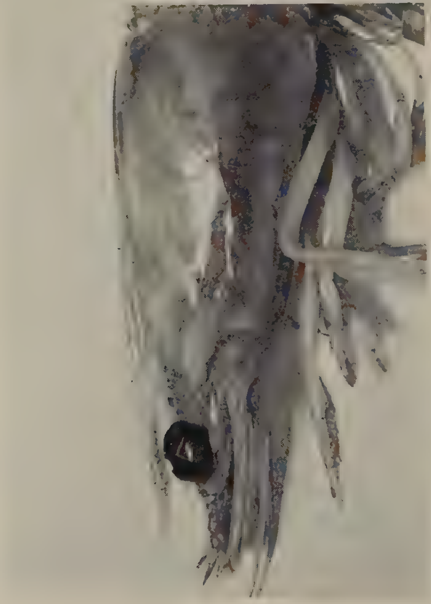
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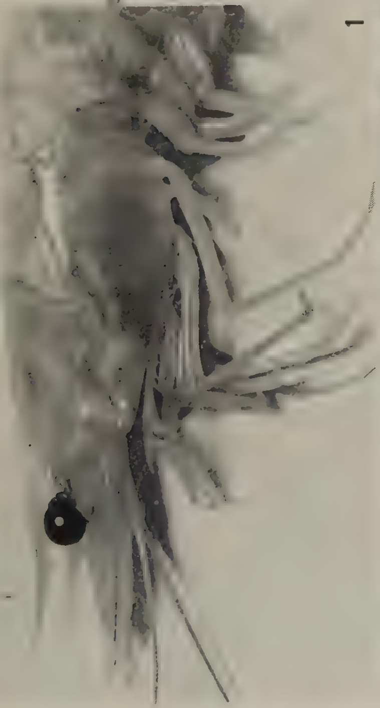

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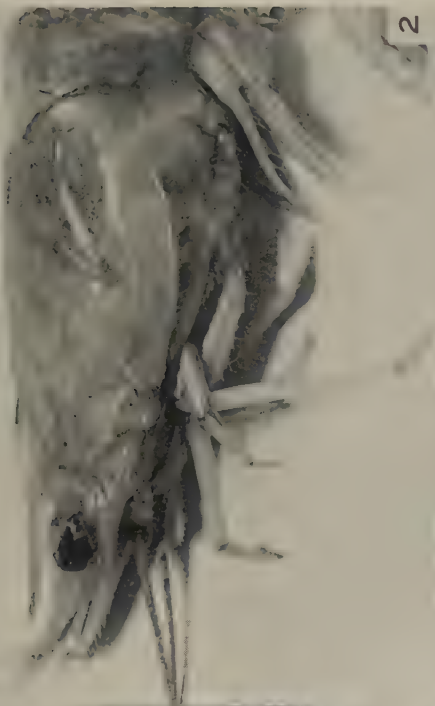

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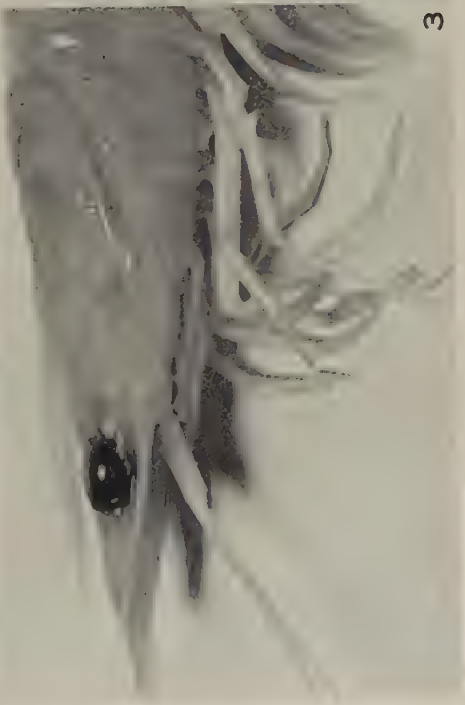

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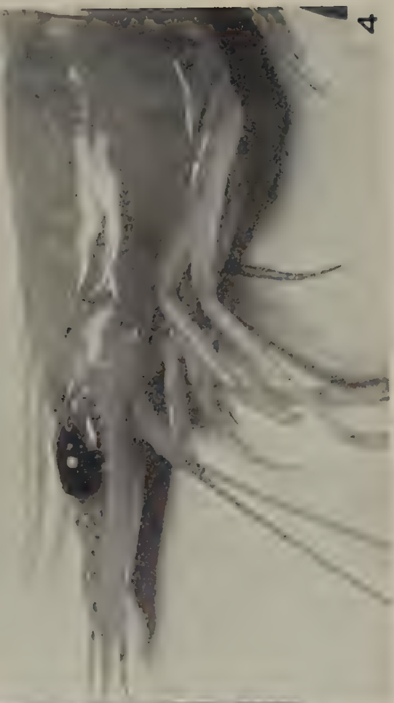

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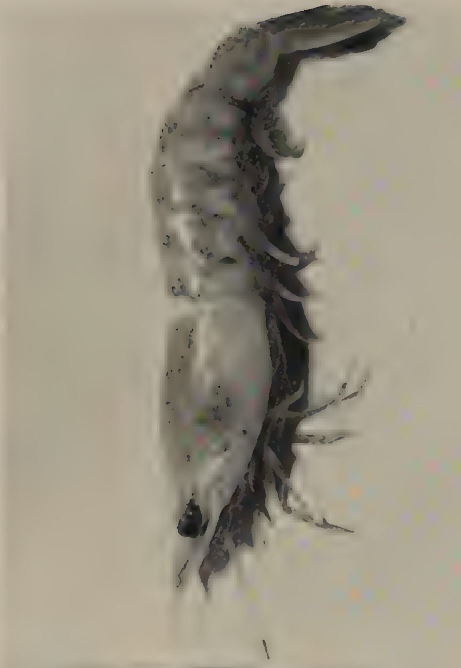

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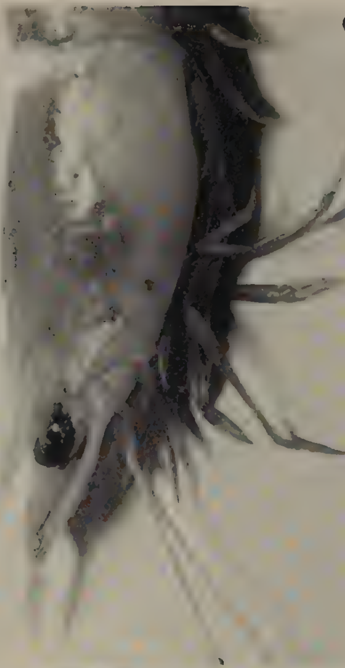

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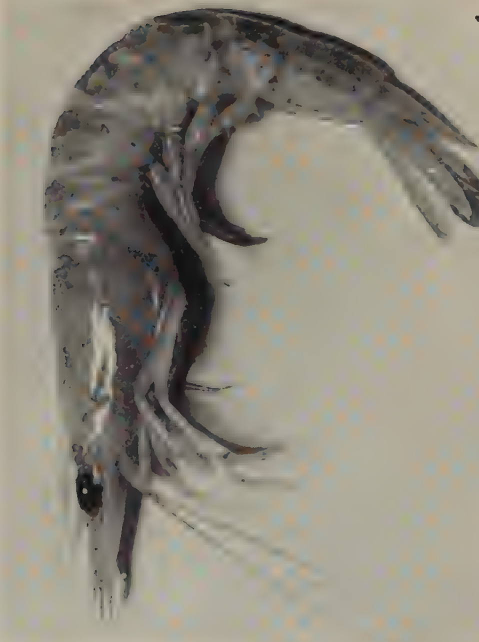

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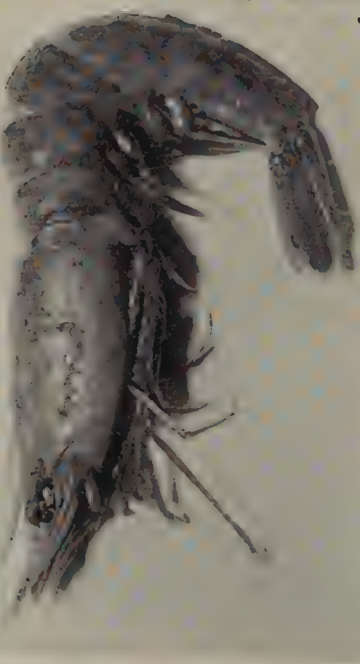

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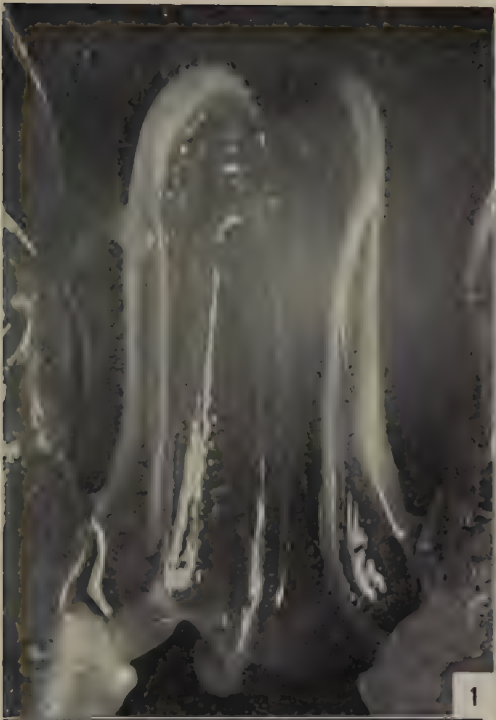

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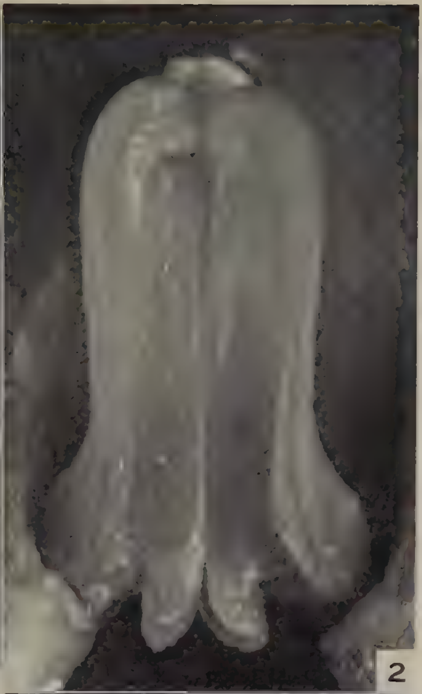

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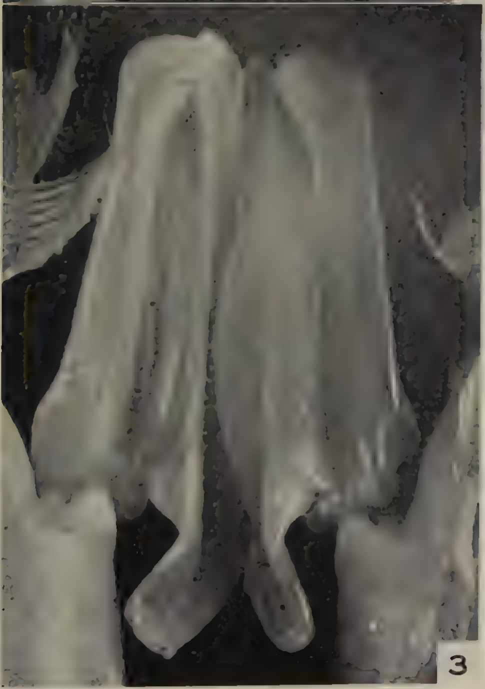

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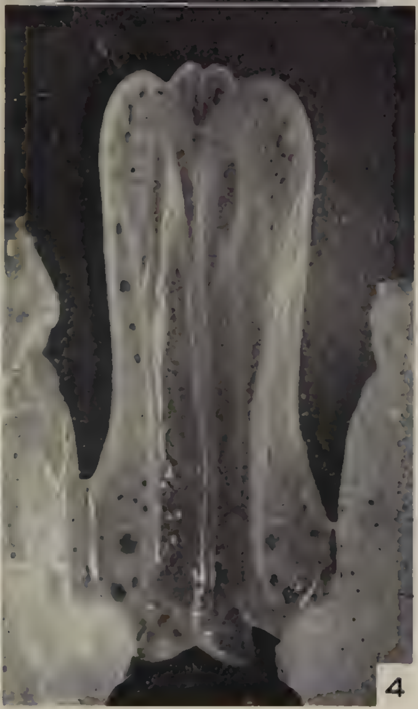

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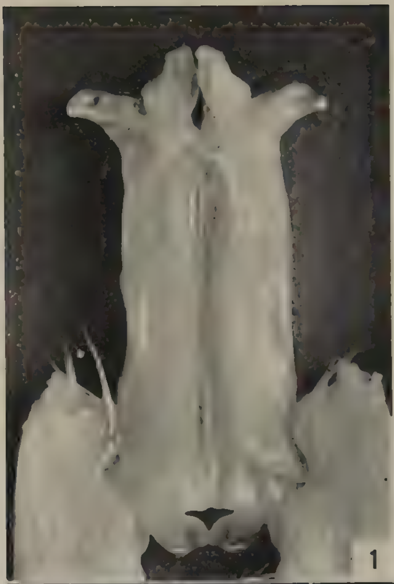
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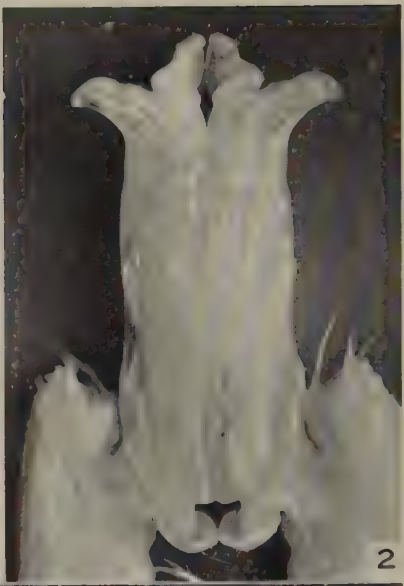
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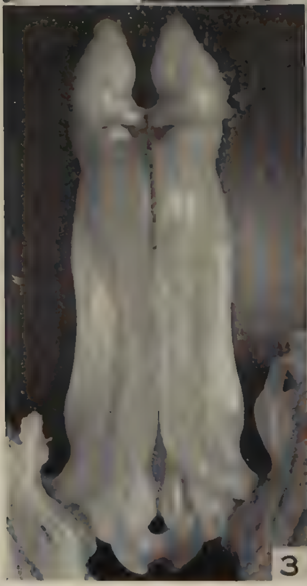
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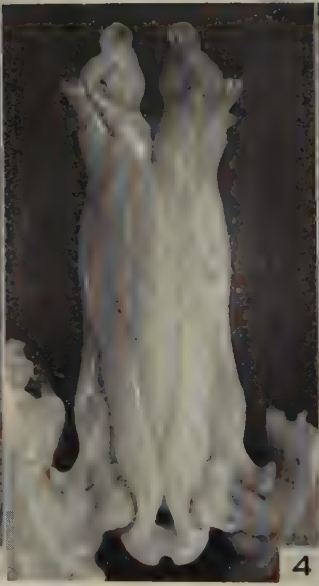
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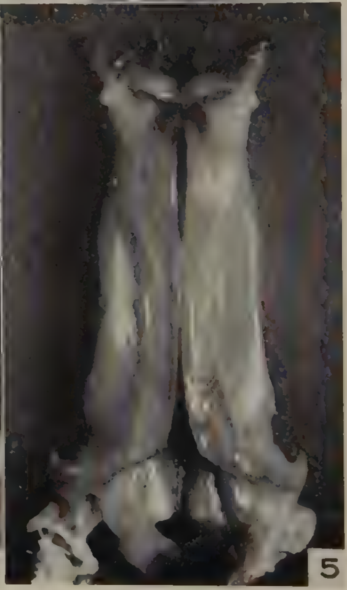
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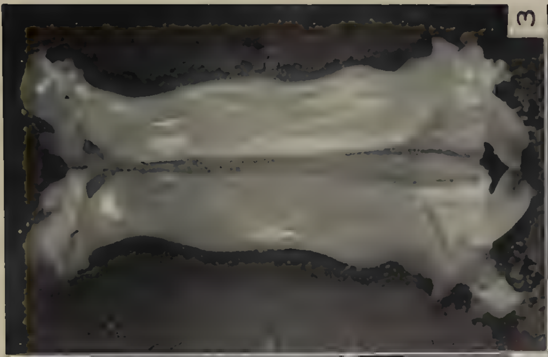
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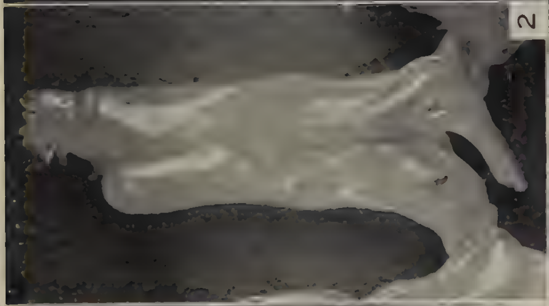
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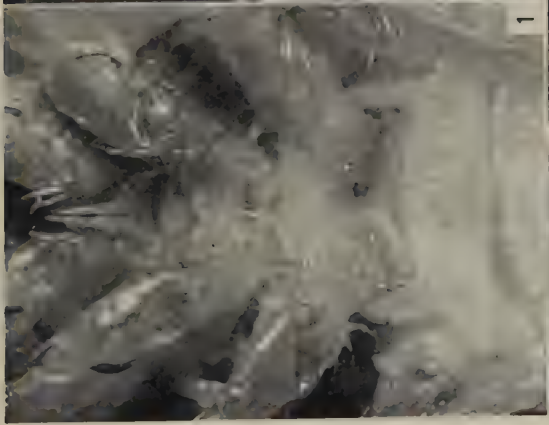
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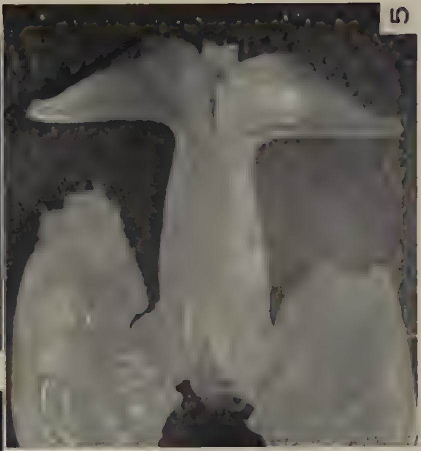
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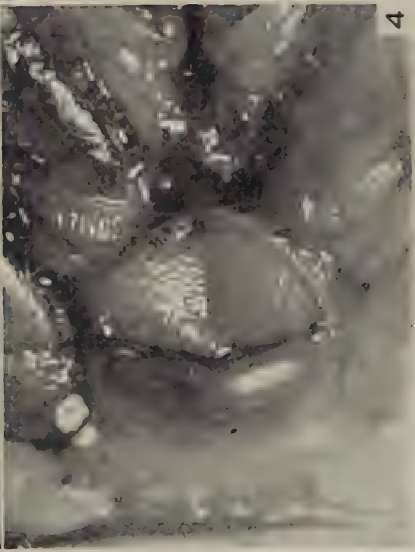
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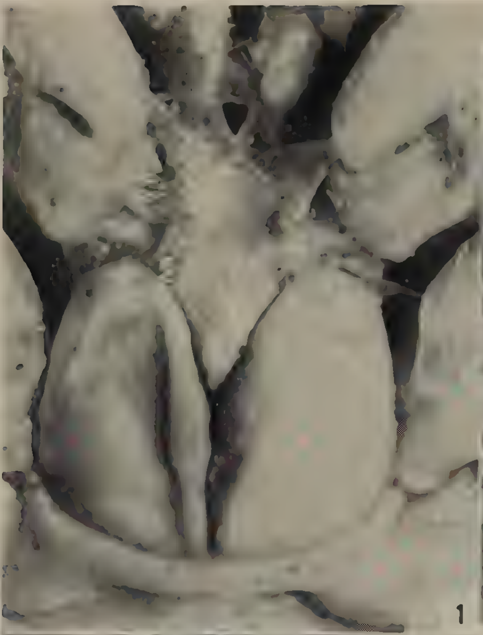
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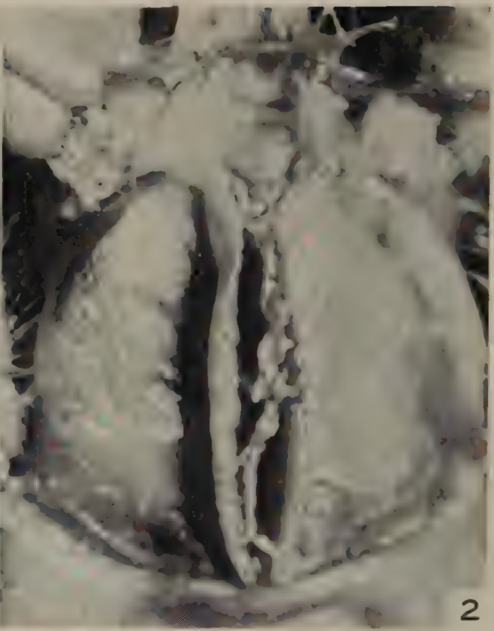
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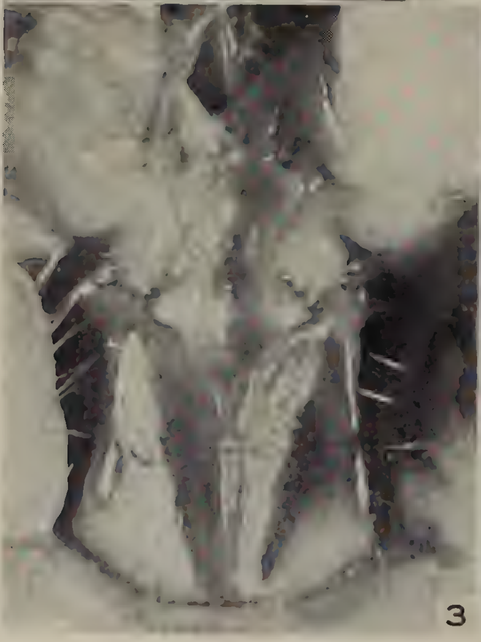
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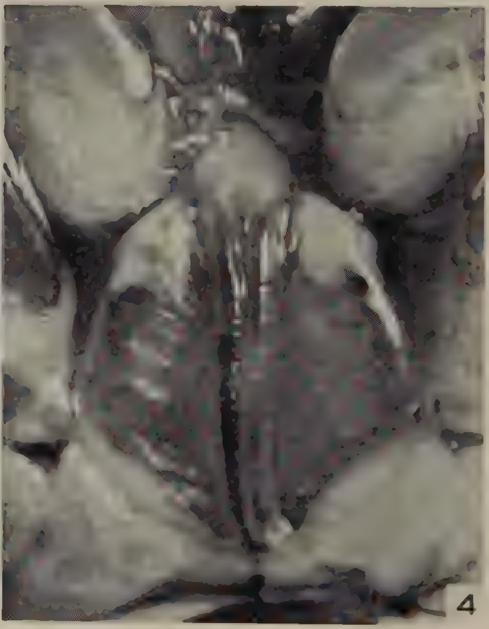
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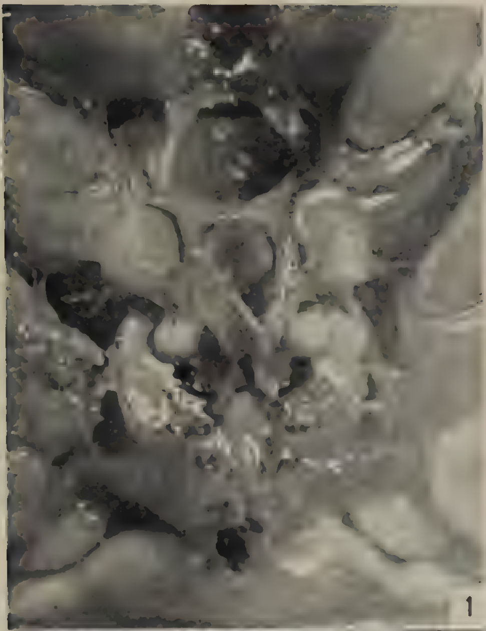
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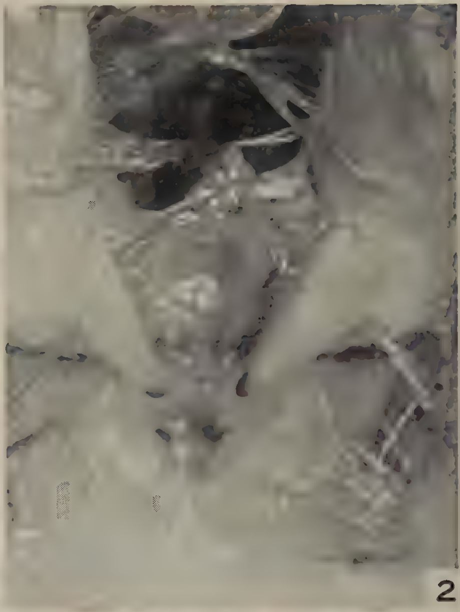
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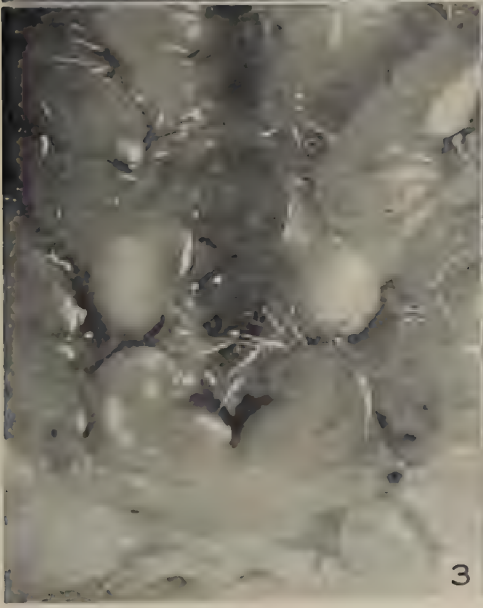
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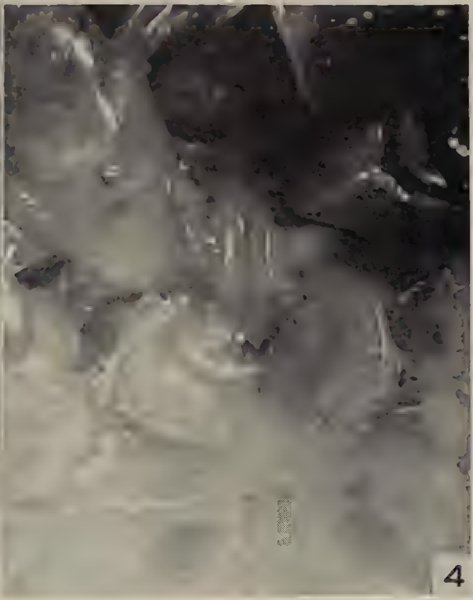
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List of Species

Genus *Metapenaeus*
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FOSSIL MICROPLANKTON FROM AUSTRALIAN LATE MESOZOIC AND TERTIARY SEDIMENTS

By GEORGES DEFLANDRE* and ISABEL C. COOKSON†

(*Manuscript received January 28, 1955*)

Summary

This paper provides the first comprehensive account of fossil microplankton assemblages from the southern hemisphere. Dinoflagellates, hystrichosphaerids, and microorganisms of uncertain affinity, all of which have unmineralized membranes, have been classified. Forty samples from bores and outcrops have been examined, and 25 genera, of which four are new, and 75 species, of which 46 are new, have been recorded from Cretaceous and Tertiary deposits. The data obtained have provided suggestive indications concerning the age of certain portions of two bores. A number of interesting facts has arisen from comparisons with the fossil microplanktons from European sediments.

I. INTRODUCTION

During the course of a palynological investigation of some Australian Tertiary continental and marine sediments one of us (Cookson 1953) observed and recorded, for the first time in Australia, the presence of planktonic organisms of both freshwater (*Pediastrum*) and salt-water origin (hystrichosphaerids).

The interest of the latter occurrence incited a special extension of these investigations to other marine deposits of the same age or older in order that a study of the microplankton as well as the microfloras contained in them might be made. About 40 samples were treated by palynological methods and several hundreds of preparations were made and examined. At the same time photomicrographs were taken of the most characteristic of the microplanktonic types.

The important collection of microorganisms thus brought together has been studied in Paris, where all the drawings and identifications have been made. The determinations and comparisons necessary for the distinction of new forms have been facilitated by two valuable aids to study in the possession of the Laboratoire de Micropaléontologie de l'École Pratique des Hautes Études:

(i) "Le Fichier Micropaléontologique Général" made and kept up to date by G. Deflandre and Mme. Marthe Deflandre-Rigaud (1943-1954). The portion of this work which is devoted to fossil microplankton contains all the published figures on this subject.

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† Botany Department, University of Melbourne.

(ii) The collection of microscopic preparations which contains, besides many holotypes, a large number of paratypes and plesiotypes from different European deposits.

A summary of the information obtained from the study of the Australian collection has already been published in Paris (Deflandre and Cookson 1954). The general and detailed results are presented below.

The lists in Section VI have been provided to facilitate comparisons and at the same time to furnish indications to those who may later take up and extend the studies inaugurated here. In this connexion it is important to note that, generally speaking, the amount of material treated from any one deposit has been relatively small, so that the lists provided should be regarded only as an indication of the composition of a microplankton assemblage and not as an exact representation of it. Future results from larger quantities of material and more exhaustive identifications will certainly considerably enlarge our knowledge in this field.

II. GENERAL CONSIDERATIONS

The biological part played by the microscopic organisms of the marine plankton is fundamental and the study of the living phytoplankton and zooplankton is one of the bases of oceanographic and marine biological research. The primordial role of the microplankton dates back to the origin of marine life, so that the study of fossil forms is of considerable interest and stratigraphical value.

Amongst the organisms of the microplankton, which constitute the food of larger animals and form "the base of the pyramid of life" in the sea, some have mineralized shells or skeletons (coccolithophorids, Foraminifera, diatoms, and Radiolaria), while others are naked or have unmineralized membranes composed solely of organic material. Remains of the former group, as has been shown in an introductory work on this subject by Deflandre (1941), have contributed largely to the formation of the sedimentary rocks, but although the group has been known for a long time, only the Foraminifera have been much studied in detail.

Most of the information regarding microorganisms with organic membranes or thecae is of recent origin and due entirely to European investigators, particularly those of France and Germany. Outside Europe this subject has scarcely been touched. No publications have appeared from Asia or Africa and only the preliminary note already cited (Cookson 1953) from Oceania. Rare information dating from the last century is all that is at present available from the American continent, but some publications are now in preparation and others have been announced.

The first non-mineralized microplankton fossils were seen in German flints by Ehrenberg more than a century ago, and during the same period several English naturalists (Reade, White, and Wilkinson) also became interested in them. However, it was not until after the first works of

O. Wetzel (1933) in Germany and G. Deflandre (1934) in France that their further study was seriously undertaken.

The siliceous medium which ensures that these organic microfossils are so well preserved is not the only one suited to their fossilization. In 1935 Eisenack isolated organisms with organic and silico-organic membranes from Jurassic calcareous sandstones by simple treatment with hydrochloric acid (Eisenack 1935, 1936). Finally Deflandre (1938), in discovering a fine Jurassic microplankton in marls and clays, demonstrated that large numbers of perfectly preserved microorganisms may be contained in sedimentary rocks of varied chemical composition.

Great progress has since been achieved, non-mineralized microorganisms now being known from the Cambrian (Eisenack 1951) onwards.

When considered as an ensemble these microfossils fall into two groups:

(1) Protista having living representatives and thus a clearly defined systematic position. Such are the members of the class Dinoflagellata of the Phytoflagellata, a revision of the numerous fossil types of which has recently been published (Deflandre 1952*a*).

(2) Protista and other microorganisms the systematic position of which is not yet clear. These forms must have been very numerous in the past since their remains are to be found abundantly in sedimentary rocks of various ages. The most important family is the Hystrichosphaeridae (name created by O. Wetzel in 1933) which has recently been revised by Deflandre (1952*b*) and Eisenack (1954). Eisenack has now proposed that the family Hystrichosphaeridae should be regarded as one of several families comprising the order Hystrichosphaeridea.

For the dinoflagellates the classification of the living forms provides a good basis and guide for the identification of the fossil types. Some of the dinoflagellates have apparently homogeneous membranes* or thecae; others have a system of external polygonal plates, the form, number, and arrangement of which provide the plate formula or tabulation characteristic of the various genera and species. The presence of a more or less deeply grooved transverse girdle (housing the undulant transverse flagellum) and the less characteristic longitudinal furrow (housing the longitudinal flagellum) generally permits the easy recognition of dinoflagellate remains.

The most ancient dinoflagellates known come from the Jurassic. In the deposits of this period, as in those of later ones, types analogous to living forms occur together with others that appear to be peculiar to the particular period.

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* The cell membrane of both fresh- and salt-water dinoflagellates is composed of cellulose, the anisotropy of which is easily seen in polarized light. This anisotropy has completely or almost completely disappeared from the membranes of the fossil forms, the cellulose having undergone a kind of condensation to a higher molecular weight with a preponderance of the amorphous phase at the expense of the crystalline phase (Deflandre 1938). Because of this change the specific tests used for living celluloses are of no use for fossil celluloses.

The Hystrichosphaeridae on the other hand cannot be associated with living forms, so that they have to be classified on a purely morphological basis. For their identification use to the maximum must be made of all the characters of form, structure, and ornamentation of the globular shell and the appendages with which most species are provided.*

The hystrichosphaerids are very ancient organisms, their remains having been recognized in Cambrian and more doubtfully in Pre-Cambrian rocks.†

The first Silurian species were described by Eisenack in 1931 and since then a considerable number of different types have been isolated from Palaeozoic deposits. In Europe hystrichosphaerids are now known from all geological periods.

The Australian Tertiary and Cretaceous sediments have furnished examples of the Dinoflagellata and Hystrichosphaeridae, and of genera of completely obscure systematic position which can be classed only as Incertae Sedis.

III. Treatment of Material

The organisms to be described in this paper occur in preparations primarily intended for pollen and spore studies, so that the methods of isolation used differ considerably from those adopted in the past by specialists in the field of fossil microplankton.

The marine or estuarine sediments treated have been mostly soft, fine-grained, carbonaceous sands and clays but a few more strongly compacted coaly deposits have been investigated.

For non-calcareous sands and clays the following procedure was followed. A small quantity of the fine powder obtained by sieving the previously pulverized sediment through a 120-150 B.S.S. was boiled in hydrofluoric acid for about 10 min and allowed to stand overnight. After washing with 7 per cent. hydrochloric acid, several changes of distilled water, and one of glacial acetic acid, the sediment was chlorinated in a solution containing 4 c.c. glacial acetic acid, 1 c.c. hydrochloric acid, and a few drops of saturated sodium chlorate solution. The residue, after washing with glacial acetic acid, was brought to the boil in a mixture consisting of 9 c.c. of acetic anhydride and 1 c.c. of concentrated sulphuric acid, after which it was washed in acetic acid and then with distilled water. At this stage a quick treatment with 10 per cent. sodium hydroxide solution was sometimes found advantageous. Finally the residue, after standing a few minutes in a 50 per cent. solution of glycerine and water, was mounted in safranin glycerine jelly.

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* For the affinities of the Hystrichosphaeridae which cannot be discussed here, "Le problème des Hystrichosphères" (Deflandre 1947) and the recent paper by Eisenack (1954) should be consulted.

† Deflandre (1948) admits that the minute organisms from the Pre-Cambrian of Bretagne (France) considered by L. Cayeux as Radiolaria belong to this group.

Calcareous clays and sands containing a high percentage of Foraminifera were treated either by the method just described, in which case the shells of the Foraminifera, coccoliths, etc., were retained in the form of calcium fluoride, or were pretreated with dilute hydrochloric acid to remove the calcareous matter and thus increase the concentration of the non-calcareous components.

For indurated deposits such as those from the Era River district, Papua, and the deeper regions of the Nelson Bore the Erdtman chlorination acetolysis method had to be replaced by treatment with Schultz's macerating solution. The powdered material was sieved and treated with hydrofluoric acid as before, then after several washings with distilled water it was allowed to stand in concentrated nitric acid, to which a few crystals of potassium chlorate had been added, for at least 24 hr at room temperature. After several changes of distilled water and treatment with a 10 per cent. sodium hydroxide solution, followed by several washings with distilled water, the residue was mounted in glycerine jelly in the usual manner.

IV. Location and Age of Sediments

Locations of deposits are listed below and shown in Figure 1.

NEW GUINEA: Era River district, Papua. Hard coaly deposits. Australasian Petroleum Company's samples L.P.E.821 and W.451, beneath Eocene and Miocene limestones. Age: Lower Cretaceous.

NEW SOUTH WALES: Onepah Station, near Tibooburra. Soft fine-grained grey sandstone, dug from a well at an unspecified depth. Age: Lower Cretaceous (*fide* Mr. H. O. Fletcher and Mr. E. J. Kenny).

WESTERN AUSTRALIA: Gingin, Molecap Hill. Lower Greensand. Age: Upper Cretaceous (Middle Senonian, Teichert 1946).

Hay-Denmark railway deviation at 354 miles (referred to hereafter as "near Denmark"). "Coffee rock" from W.A. Railways Dept. bore No. 9, between 18 and 27 ft. Age: probably Lower Tertiary (Cookson 1954*b*). Geol. Dept. Univ. W.A. No. 8662/9.

VICTORIA: Nelson, Parish of Glenelg. Carbonaceous sediments occurring at intervals between 992 and 6192 ft, from Vic. Dept. of Mines bore, SW. end of bridge over Glenelg River. Age: Probably Lower Eocene to Upper Cretaceous.

Princetown-Moonlight Head district (Fig. 59):

(*a*) Pebble Point Formation. Basal grits, Wangerrip Group. From NW. side of Point Bell, 2¾ miles SE. of mouth of Gellibrand River near Princetown. Age: Paleocene to Lower Eocene (Baker 1953). Melb. Univ. Geol. Dept. No. 3396.

(*b*) Upper part of Dilwyn Clay, Wangerrip Group. 1 mile SE. of mouth of Gellibrand River. Carbonaceous sandy clay. Age: Lower Eocene (Baker 1953).

(*c*) Princetown Member of the Dilwyn Clay near mouth of Gellibrand River, about ¾ mile SE. of Point Ronald. Carbonaceous sandstone. Age: Lower Eocene (Baker 1953).

(*d*) Gellibrand Clay, Heytesbury Group, 2¼ miles NW. of mouth of Gellibrand River. Age: Middle Miocene (Balcombian, Singleton 1941, p. 25; Baker 1944, p. 98).

Birregurra bore No. 1:

(*a*) Carbonaceous clays from Vic. Dept. of Mines bore No. 1, between 760 and 900 ft (Cookson 1954*a*, p. 126). Age: ? Lower Eocene.

(*b*) Dark grey clays from Birregurra bore No. 1, between 444 and 449 ft and 514 and 516 ft. Age: Miocene or older.

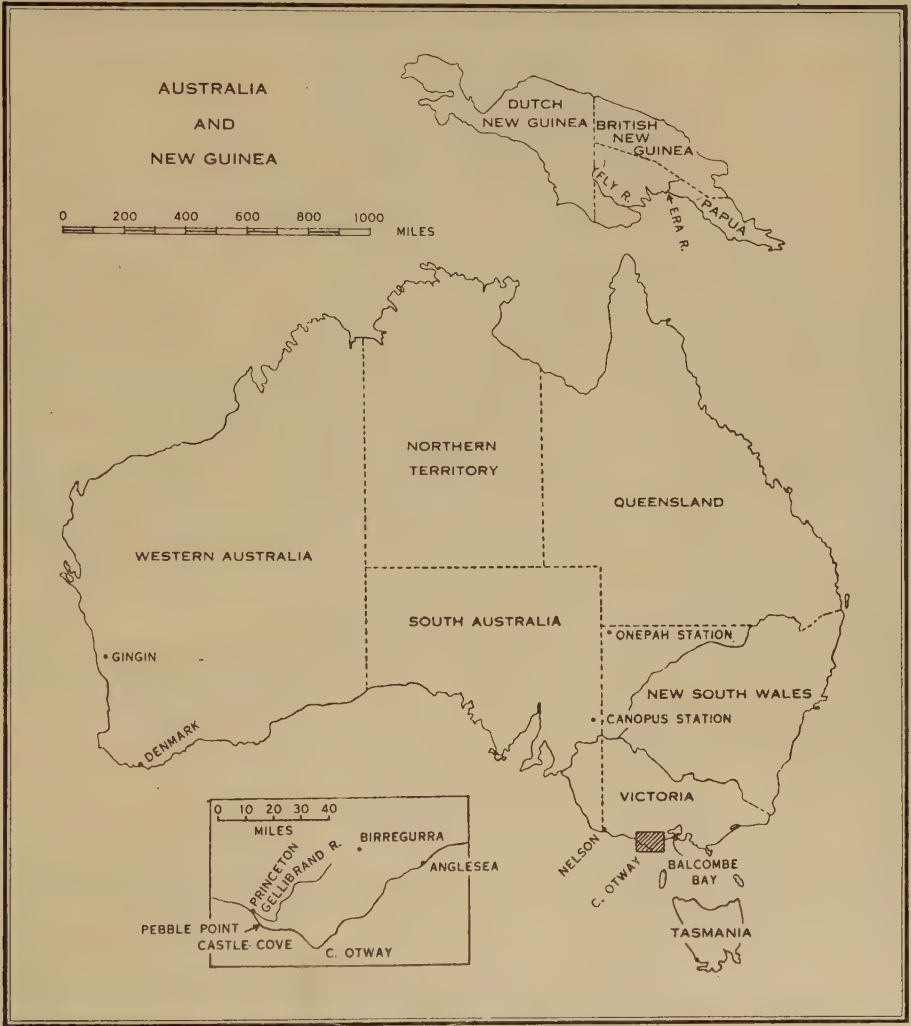

AUSTRALIA
AND
NEW GUINEA
0
200
400
600
800
1000
MILES
DUTCH
NEW GUINEA
BRITISH
NEW
GUINEA
FLY R.
ERA R.
PAPUA
NORTHERN
TERRITORY
QUEENSLAND
WESTERN AUSTRALIA
SOUTH AUSTRALIA
ONEPAH STATION
GINGIN
NEW SOUTH WALES
CANOPUS STATION
DENMARK
VICTORIA
0
10
20
30
40
MILES
BIRREGURRA
PRINCETON
GELLIBRAND R.
ANGLESEA
PEBBLE POINT
CASTLE COVE
C. OTWAY
NELSON
C. OTWAY
BALCOMBE
BAY
TASMANIA

Fig. 1.—Map showing the location of deposits in which microplanktonic assemblages have been found.

Anglesea. Black carbonaceous sandstone from coastal cliff near mouth of Anglesea River. Age: ? Middle Eocene (Raggatt and Crespin 1952, p. 146).

Castle Cove, Aire coast. Basal clay of the Castle Cove section. Age: Upper Eocene or older (*fide* Dr. O. P. Singleton).

Balcombe Bay. Grey shelly marls. Age: Middle Miocene (Singleton 1941, pp. 63-4).

Hampton, near Melbourne. Black carbonaceous sandstone at base of coastal cliff, about 100 yd south of Hampton Life Saving Club. Age: post-Cheltenhamian (post-Upper Miocene) (*fide* H. T. Clifford).

SOUTH AUSTRALIA: Canopus Station, near S.A. and N.S.W. border, *c.* 45 miles N. of Murray River. Carbonaceous sandstone from the S.A. Dept. of Mines bore at 548-925 ft. Age: Eocene (probably Lower Eocene (Cookson, unpublished data)).

V. Systematic Classification

Class **DINOFLAGELLATA**

Family **GYMNODINIDAE**

Genus GYMNODINIUM Stein

GYMNODINIUM cf. HETEROCOSTATUM Deflandre

Plate 1, Fig. 7

Gymnodinium heterocostatum Deflandre, 1935, Bull. Biol. 69: 226, fig. 6.

Upper Cretaceous (Senonian): Gingin, W.A.

The principal character of *G. heterocostatum* Defl. (1936), that is, the alternation of ridges of 2 different sizes, has only been observed on the hypotheca of 1 of the 2 specimens observed. The general shape of both is less elongated than in the type and nearer to that of *G. cretaceum* Defl., but the dimensions, length 58-61 μ and breadth 48-54 μ, are considerably higher than those of the latter species. Perhaps the Gingin specimens represent a new species: however, the material is insufficient for such an exact determination.

Types.—Holotype: Coll. G. Deflandre, AF58.

It is significant to find in an Australian deposit a form so similar to the European species of *Gymnodinium* with longitudinal ridges, namely, *G. heterocostatum* Defl., *G. cretaceum* Defl., *G. decorum* Defl., and *G. avellana* Lej.-Carp., present in Cretaceous flints.

GYMNODINIUM AUSTRALIENSE sp. nov.

Plate 5, Fig. 1

Middle Miocene (Balcombian): Balcombe Bay, Vic., and Gellibrand Clay, near Princetown, Vic.

Miocene or older: Birregurra, Vic., bore No. 1 at 444-449 ft, 514-516 ft.

Cell globular, divided into 2 approximately equal parts by a narrow, rather shallow, strongly helicoidal girdle. A longitudinal furrow is visible on the hypotheca. The epitheca is surmounted by a short truncate process, the centre of which is frequently depressed. Usually the base of the process is distinctly mammilate. Hypotheca widely rounded; both parts or only the epitheca are bell-shaped. The membrane is finely punctate and sometimes indistinct lines suggestive of plates are apparent. The cell is generally encysted with a more or less quadrangular opening on the dorsal face of the epitheca.

Dimensions.—Total length 102-105 μ, breadth 87-105 μ.

G. australiense seems to be more abundant in the material from the type locality at Balcombe Bay than in the sample from the Balcombian horizon near Princetown. It does not resemble any known living species but rather approaches the Jurassic species *G. crystallinum* Defl. However, the apical regions of the two species are quite distinct.

Family **DEFLANDREIDAE**

Genus DEFLANDREA Eisenack

DEFLANDREA PHOSPHORITICA Eisenack

Plate 3, Fig. 5

Deflandrea phosphoritica Eisenack, 1938, Schr. Phys.-ökon. Ges. Königsb. 70: 183, fig. 6.

? Lower Eocene: Birregurra, Vic., bore No. 1 at 876-877 ft.

This species is now well known and its variations seem to be of little importance. The widely conical epitheca is surmounted by a more or less well-developed horn-like process. The 2 antapical horns are often unequal and may be reduced to 2 slightly prominent protuberances.

The Australian examples are quite similar to the type from the Lower Oligocene of Samland (East Prussia) with which they have been compared (collections of A. Eisenack at Reutlingen and G. Deflandre at Paris).

Dimensions.—Total length 100-128 μ, breadth 69-95 μ.

Types.—Holotype: A. Eisenack, Reutlingen, Ph. 44. Paratype: Coll. G. Deflandre, Paris, AV99.

The stratigraphical and topographical distribution of *D. phosphoritica*, as at present known, is as follows:

Lower Eocene: Ypresian, Wytschaete, Belgium (Reissinger 1950).

? Lower Eocene: Birregurra, Vic., Australia (Cookson 1954*a*).

Upper Eocene: Bore Wöhrden, Holstein, Germany (Klumpp 1953).

Lower Oligocene: Amber Formation, Samland, East Prussia (Eisenack 1938*a*).

Middle Oligocene: Rupelien (Septaria clays), Innien, Holstein, Germany (Deflandre, unpublished data).

DEFLANDREA HETEROPHLYCTA sp. nov.

Fig. 5; Plate 5, Fig. 6

Upper Eocene or older: Castle Cove, Vic. (holotype in collection of G. Deflandre, BX36).

Epitheca broadly conical with slightly convex flanks and a somewhat rounded, unthickened apex; hypotheca a little smaller than the epitheca and provided with 2 short, blunt, slightly divergent horns. Transverse girdle clear but shallow. Cyst spheroidal, ornamented with irregularly dispersed tubercles more numerous and coarser towards the poles. Cyst membrane finely punctate. Opening laterally extended situated towards the apical pole. Membrane of theca very finely and sparsely punctate.

Dimensions.—Total length 115 μ, breadth 80 μ; cyst 70 by 72 μ.

The general form of this species recalls *D. phosphoritica* Eis. but it is clearly distinct in the tuberculate ornamentation of the cyst.

This description is based on the single specimen constituting the holotype. However, thanks to the clear information it has supplied, it has been possible to recognize isolated cysts of *D. heterophlycta* in the same material and to study their variations.

Some of the cysts are identical with the one still contained in the normal dinoflagellate theca. The one shown in Plate 5, Figure 6, shows a considerable enlargement of some of the polar tubercles, which may attain dimensions of as much as 13 by 5 μ, but like the smaller tubercles they are always solid and have a granular surface. The wall of the cyst is also very finely and irregularly punctate. All the cysts possess an aperture beneath the apical pole.

This is the first time that it has been possible to precisely place in a genus of the Dinoflagellata a microfossil which, as an isolated unit, would perhaps have been classified in the Hystrichosphaeridae.

The cyst of *D. heterophlycta* by its morphology could have found a place in the genus *Leiosphaera* Eisenack—a precarious position, however, because in the development of the polar tubercles it would also have approached the genus *Hystrichosphaeridium.*

This example shows that we may still hope to improve our knowledge of those microfossils to which an exact systematic position cannot be given and which at present are provisionally relegated to Incertae Sedis.

DEFLANDREA ROBUSTA sp. nov.

Plate 4, Fig. 9

Lower Eocene: Princetown Member of the Dilwyn Clay, Vic.

Theca with widely convex sides, a regular conical apex, and 2 strong, conical, non-divergent antapical horns. Transverse girdle marked by the thickness of its edge, not depressed, separating the theca into 2 nearly equal parts. Membrane smooth with only a few very fine granulations. Cyst ellipsoidal, flattened, smooth.

Dimensions.—Length 123 μ, breadth 74 μ.

This species, unfortunately represented by only a single specimen, is well characterized. It possesses an epitheca analogous to that of *D. bakeri* (described below) and a hypotheca with 2 horns similar to those of *D. phosphoritica* but proportionally narrower. The membrane is quite distinct from that of *D. bakeri.*

DEFLANDREA BAKERI sp. nov.

Plate 4, Figs. 1, 2, and 4

Paleocene to Lower Eocene: Pebble Point Formation, Vic.

Cell generally but not always encysted. Theca widely fusiform, somewhat obliquely truncated posteriorly; transverse girdle faint, neither hollowed nor shallow, sometimes quite indistinct, dividing the theca into 2 unequal parts. Longitudinal furrow not observed. Epitheca larger than the hypotheca, widely conical or bell-shaped, surmounted by a short, more or less bluntly pointed, slightly thickened prominence. Hypotheca like a frustum of a cone, sometimes with 2 very short unequal horns and occasionally a 3rd submedian conical expansion, sometimes with the lower angles simple or 1 of the 2 rounded. In lateral view (Plate 2, Fig. 4) the encysted cells have an asymmetrical outline with, at the level of the cyst, 1 face plane and the other convex. This convexity does not seem to exist in the rare non-encysted examples that have been examined. The cyst also causes a slight frontal enlargement.

The cyst is ellipsoidal, more or less regular when viewed from the front, more asymmetrical in lateral view. The encysted cells have a rather regular polygonal aperture on the convex side of the epitheca.

Membrane of the theca more or less strongly and irregularly punctate, except in the region of the transverse girdle, where it is generally smooth.

Dimensions.—Holotype (Plate 3, Fig. 2): theca, length 108 μ, breadth 61 μ; cyst, length 51 μ, breadth 56 μ. Range: theca, length 87-108 μ, breadth 54-69 μ; cyst, length 41-50 μ, breadth 50-56 μ.

This description applies to the form considered as typical which has only been found in the Pebble Point Formation. At this locality a series of individuals has been observed with thinner, more finely punctate membranes which perhaps correspond to young forms. However, the exclusive presence of similar forms in the Nelson Bore at 3874 ft has led to their being provisionally distinguished from the type under the name forma *pellucida*.

DEFLANDREA BAKERI forma PELLUCIDA f. nov.

Plate 4, Fig. 3

? Paleocene to Lower Eocene: Nelson Bore, Vic., at 3874 ft (type).

Paleocene to Lower Eocene: Pebble Point Formation, Vic.

Membrane of the theca thinner and more finely punctate than that of the type. Outline not especially enlarged in the region of the cyst. Posterior end simply and obliquely truncate, slightly depressed in the middle.

Dimensions.—Type (Plate 2, Fig. 3): theca, length 118 μ, breadth 77 μ; cyst, length 67 μ, breadth 74 μ. Other specimens: length up to 113 μ, breadth up to 92 μ.

DEFLANDREA OBLIQUIPES sp. nov.

Plate 4, Fig. 6

Lower Eocene: Princetown Member of the Dilwyn Clay, Vic. (type).

Paleocene to Lower Eocene: Pebble Point Formation, Vic.

Theca with a somewhat pentagonal outline. Transverse girdle hollowed, longitudinal furrow not observed. Epitheca conical, surmounted by a strong, truncate or rounded horn. Hypotheca like a frustum of a cone with short, straight flanks, a wide flat base and a stout, divergent process at each angle. Cyst rounded-pentagonal. Opening on epitheca apparently triangular with a rounded apex. Membrane of both cyst and theca finely punctulate.

Dimensions.—Overall length 100-108 μ, breadth 69-79 μ, apical horn *c.* 28 μ, basal horns *c.* 20 μ.

This curious species has the general appearance of certain types of living *Peridinium* and species of *Palaeoperidinium* from Cretaceous flints (O. Wetzel 1933, Plate 11, Fig. 14; Deflandre 1936, Plate 4, Fig. 7).

DEFLANDREA PACHYCEROS sp. nov.

Plate 4, Fig. 7

Lower Eocene: Princetown Member of Dilwyn Clay, Vic., and upper part of Dilwyn Clay, Vic.

Cell encysted, polygonal with a shallow transverse girdle, epitheca and hypotheca about equal. Epitheca widely conical, terminated by a slightly truncate apex; hypotheca provided with 2 strong, somewhat divergent, conical horns with straight or slightly concave sides and blunt apices.

Cyst ellipsoidal, tending in the type (Plate 4, Fig. 7) to protrude towards the apex. Membrane of theca entirely covered with small spines or warts.

Dimensions.—Length 89 μ, breadth (56) 64 μ.

The lateral position in which the holotype is lying reduces its breadth (56 μ).

DEFLANDREA sp.

Plate 4, Fig. 8

Lower Eocene: Princetown Member of the Dilwyn Clay, Vic.

Theca consisting of a central globular part, a conical apex, and 2 widely separated, conical, pointed antapical horns. Transverse girdle indistinct. Cyst spheroidal, smooth. Membrane of theca irregularly strewn with very fine granules.

Dimensions.—Length *c.* 92 μ, breadth *c.* 59 μ.

The single specimen of this type available is insufficiently well preserved to serve as the type of a new species. However, it has characters distinct from those of all other forms of *Deflandrea* which will permit it to be recognized when the species to which it belongs is precisely described.

Genus WETZELIELLA Eisenack

According to Eisenack's conception of the genus *Wetzeliella* the theca always contains a clearly defined cyst with a distinct membrane, the individual species being characterized by the form and aspect of the theca itself (Eisenack 1935, 1936, 1954).

The first of the two Australian forms to be referred to *Wetzeliella* and to be described below, *W. lineidentata* sp. nov., has this typical constitution, but the structure of the cell membrane and especially its rather regularly disposed ornament distinguish it from the other species of *Wetzeliella*. The flattened form of the organism and its general outline, which is close to that of *W. clathrata* Eis., appear to justify its reference to this genus.

The second species, *W. homomorpha* sp. nov., never seems to possess a·cyst, a feature which precludes its reference to *Wetzeliella* as originally defined. However, several reasons can be given for the wider conception of *Wetzeliella* adopted here and the inclusion in the genus of the Australian species *W. homomorpha*. Firstly, the general appearance of the theca and the constant structure and disposition of the processes are both similar to those found in *Wetzeliella*. Secondly, some otherwise typical examples of the fossil dinoflagellate *Deflandrea bakeri* have no cyst, a fact that has strengthened the opinion that the presence or absence of a cyst is a biological character rather than a morphological character of great systematic value. Moreover, one of us (Deflandre, unpublished data) has noticed that in unquestionable examples of *Wetzeliella* from the Oligocene of Innien, Germany, the cyst membrane may be extremely delicate and much thinner than the membrane of the theca, and has also observed the same feature in certain paratypes of *W. articulata* (genotype).

WETZELIELLA LINEIDENTATA sp. nov.

Figs. 17 and 18; Plate 5, Fig. 5

Probably Lower Tertiary: near Denmark, W.A.

Cell encysted, compressed, nearly quadrangular with a toothed margin. Epitheca imperfectly preserved, probably triangular, opening apparently quadrangular; hypotheca with 2 short unequal horns. Membranes of cyst thick, roughened. Cell membrane with lines of numerous short, blunt teeth, in surface view relatively widely spaced both equatorially and so as to delimit roughly polygonal areas analogous to the plates characterizing the Peridinales.

Dimensions.—Overall length 118 μ, breadth 110 μ; cyst, length 84 μ, breadth 77 μ.

This unique specimen, although incomplete, merits description because of its distinctness from all other known species of *Wetzeliella*. It is of special interest on account of the alignment of the small spines, as drawn in Figures 16 and 17, not only in the equatorial zone but so as to form a kind of tabulation, both dinoflagellate characters. With more material the details of the tabulation will doubtless become more precisely determined.

It does not appear possible to demonstrate such a clear arrangement of the ornamentation in the known species of *Wetzeliella*. The most that can be said at present is that in *W. articulata* (O. Wetzel) Eis. a certain alignment of the processes in the equatorial zone does exist. One of us, rejecting the opinion of Pastiels (1948), has already replaced *Wetzeliella* in the Dinoflagellata (Deflandre 1952*a*), a position accepted by Eisenack (1954) in his latest study of several new types. The structure of *W. lineidentata* definitely supports this position.

WETZELIELLA HOMOMORPHA sp. nov.

Figs. 17 and 18; Plate 5, Fig. 7

Hystrichosphaeridium geometricum Pastiels, sec. Cookson, 1953, pl. 2, fig. 25, non *H. geometricum* Defl. *Hystrichosphaeridium geometricum* Pastiels, 1948 pars.

Lower Eocene: Princetown Member of Dilwyn Clay, Vic.

Theca compressed, outline polygonal or more or less rounded, furnished with short, simple or bifurcate processes sometimes associated in small groups, generally more numerous at the edge of the theca. Membrane with a smooth surface.

Dimensions.—Diameter of shell (not counting appendages) 44-60 μ, processes 5-15 μ long.

This form, as has already been stated (Cookson 1953), is probably identical with one of the types of *Hystrichosphaeridium geometricum* Pastiels (1948, Plate 4, Fig. 8). But the name created by Pastiels is preoccupied by *H. geometricum* Defl. (1942), and cannot be used for the species removed to the genus *Wetzeliella* ("Botanical Rules of Nomenclature," art. 60).

None of the Australian examples has contained the internal cyst characteristic of the genus. On the other hand the drawings of two of Pastiels' specimens (Plate 4, Figs. 2 and 3) seem to indicate that a cyst was present.

Family **GLENODINIDAE**

Genus PALAEOGLENODINIUM Deflandre

PALAEOGLENODINIUM sp. indet.

Plate 1, Fig. 4

Upper Cretaceous: Gingin, W.A.

Halves of two thecae which superficially resemble this genus have been observed in the preparations of the Gingin Greensand. The length of the larger is about 135 μ and the height 77 μ so that the entire theca must have been approximately 154 μ long. These dimensions are considerably greater than those of *P. cretaceum* Defl. (length 71-75 μ).

This form is cited only to show the existence of this type of dinoflagellate in an Australian Cretaceous deposit.

Family **GONYAULACIDAE**

Genus GONYAULAX Diesing

GONYAULAX cf. WETZELI Lejeune-Carpentier

Plate 1, Fig. 3

Gonyaulax wetzeli Lejeune-Carpentier, 1939, Ann. Soc. Géol. Belg. 62: B527, fig. 1.

Lower Cretaceous: Onepah Station, N.S.W.

In spite of the recognition of individual plates this identification remains uncertain because it has not been possible to determine the complete tabulation.

The general appearance of the Australian specimens is similar to that of *G. wetzeli* from Senonian flints of northern Germany, but their size is slightly larger.

Dimensions.—Length 79-92 μ, breadth 69-76 μ.

Types.—Holotype: Coll. O. Wetzel, Eutin, No. 495.

? GONYAULAX sp. indet.

Plate 1, Fig. 6

Lower Cretaceous: Onepah Station, N.S.W.

This specimen is too badly preserved for description and even its reference to *Gonyaulax* is uncertain. It deserves mention, however, because dinoflagellates with clearly defined denticulate ridges and sutures such as it possesses, although relatively frequent in the European Jurassic (*Gonyaulax jurassica* Defl., *G. eisenacki* Defl.), are rare in the Cretaceous. Only *Rhynchodiniopsis aptiana* Defl. from the Aptian of the south of France has analogous surface features.

Dimensions.—Theca, overall length 56 μ, breadth 46 μ.

Family **HYSTRICHODINIDAE**

Genus HYSTRICHODINIUM Deflandre

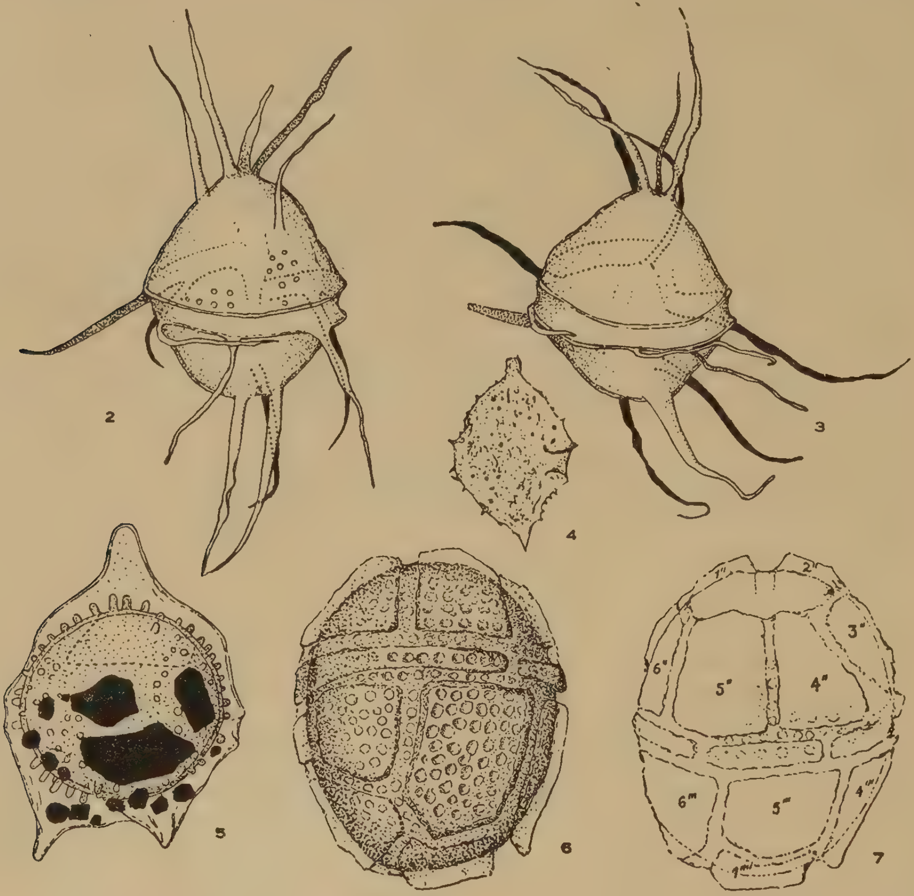
HYSTRICHODINIUM OLIGACANTHUM sp. nov.

Figs. 2 and 3; Plate 1, Fig. 1

Lower Cretaceous: Onepah Station, N.S.W.

Theca with rounded poles, epitheca a little larger than the hypotheca, the transverse girdle strongly helicoidal and left-handed with no appendages on its upper rim but 6 or 7 on its lower rim. The horns are long, often attaining the length of the theca; there are about 4 or 5 on the upper half of the epitheca and 3 to 4 on the hypotheca, the total number being approximately 14. Certain specimens, perhaps incomplete, have shown 11 or 12.

Membrane of theca clearly ornamented.



Figs. 2-3.—*Hystrichodinium oligacanthum* sp. nov. Posterior faces (dotted lines indicate the girdle of the ventral face). (Fig. 2, holotype. P16209.) Onepah Station, N.S.W. × 622. Fig. 4.—*Palaeohystrichophora minuta* sp. nov. Gingin, W.A. (type). × 622. Fig. 5.—*Deflandrea heterophlycta* sp. nov. Holotype. Castle Cove, Vic. × 390. Figs. 6-7.—*Eisenackia* gen. nov. *crassitabulata* sp. nov. in lateral view (Fig. 7, the inferior face seen through the upper). Pebble Point, Vic. × 622.

Dimensions.—Holotype (Fig. 2): theca, length 47 μ, breadth 42 μ, horns 35-42 μ, total length 117 μ. Another example: length 43 μ, breadth 40 μ, horns 39-44 μ, overall length 106 μ.

This new species clearly differs from the forms described from European Cretaceous flints in the reduced number of appendages and in the localization of so many of them on the lower rim of the transverse girdle. The ornamentation is also less strongly marked than in the type of *Hystrichodinium pulchrum* Defl. (1936).

Genus PALAEOHYSTRICHOPHORA Deflandre emend.

The type of the genus, *P. infusorioides* Defl., common in the Upper Cretaceous of the Paris basin, has not yet been found in Australia, but forms rather similar to it, although not coming within the limits of the genus as originally defined, have been met with.

It therefore now seems opportune and desirable to enlarge the description of the genus so as to include, at least provisionally, those dinoflagellates without any trace of tabulation but with the membrane clothed with more or less dense, sometimes very short spines.

The revised diagnosis of the genus *Palaeohystrichophora* should be: dinoflagellates with a generally thin theca furnished with a transverse girdle, longitudinal furrow clear or indistinct, plates absent, membrane covered with irregularly disposed, stiff or soft spines or hairs.

Besides the two new Australian species to be described below, the genus thus amended also accommodates *Palaeoperidinium spinosissimum* Defl. (Deflandre 1938, Plate 9, Fig. 11) under the name *Palaeohystrichophora spinosissima* (Defl.). *Palaeoperidinium caulleryi* Defl., however, in spite of certain resemblances cannot be placed in *Palaeohystrichophora* because of the linear arrangement of its short spines. Moreover this character indicates affinity with those forms of *Gonyaulax* with toothed sutures to which previous reference has been made (p. 255).

PALAEOHYSTRICHOPHORA MULTISPINA sp. nov.

Plate 1, Fig. 5

Upper Cretaceous (Senonian): Gingin, W.A.

Theca biconical with an approximately median, straight, probably helicoidal girdle. The portion taken as the epitheca is terminated by a short truncate process, the hypotheca being prolonged into a short, stout point. The membrane, which shows no trace of plates, is entirely covered with short spines.

Dimensions.—Length 56 μ, breadth 38 μ.

The single specimen is clearly flattened and slightly broken laterally. However, it is a well-characterized and easily recognizable form.

PALAEOHYSTRICHOPHORA MINUTA sp. nov.

Fig. 4

Upper Cretaceous (Senonian): Gingin, W.A.

Theca biconical with slightly convex sides; transverse girdle relatively wide and shallow; epitheca and hypotheca approximately equal, epitheca prolonged into a short, cylindrical, truncate process, hypotheca terminating in a short, sharp point. Membrane without trace of plates rather sparsely clothed with short, irregularly disposed spines.

Dimensions.—Length 40 μ, breadth 26 μ.

The single specimen on which this species is based (holotype) is at present the smallest of the Australian Cretaceous dinoflagellates.

PALAEOHYSTRICHOPHORA cf. SPINOSISSIMA Deflandre

Plate 4, Fig. 10

Palaeoperidinium spinosissimum Deflandre, 1938, Trav. Stat. Zool. Wimereux **13**: 179, pl. 9, fig. 11.

Palaeohystrichophora spinosissima (Deflandre) comb. nov.

Lower Eocene: Princetown Member of Dilwyn Clay, Vic.

Theca widely fusiform, the epitheca and hypotheca very unequal. Transverse girdle straight. Membrane entirely and densely covered with short spines.

Dimensions.—Length 122 μ, breadth 56 μ.

Types.—Holotype: G. Deflandre, Paris, AM46.

This specimen has been compared with the type of *P. spinosissima* which, like it, is also badly preserved. However, there is a sufficiently great resemblance in the appearance of the membrane to justify at least a provisional association of this interesting Australian Tertiary form with the type from the Jurassic of France (Oxfordian). The holotype of the latter is probably incomplete, and it will be very useful to find additional specimens of these two apparently similar morphological types.

A smaller (69 by 54 μ), more imperfect specimen that possibly affords a second example of *P. spinosissima* has been observed in the Lower Tertiary deposit near Denmark, W.A.

Family **INCERTA**

Genus EISENACKIA gen. nov.

Cell globular without appendages. Transverse girdle and longitudinal furrow not marked by a depression of the membrane, which has a completely continuous outline. Transverse girdle delimited by the bases of the plates. Tabulation 2-3′, 6″, ?6*g*, 6‴, 2*p*, 1⁗. The epitheca has, amongst others, an elongated ventral plate, and the hypotheca a ventral area consisting of several small plates.

Genotype, *Eisenackia crassitabulata* sp. nov.

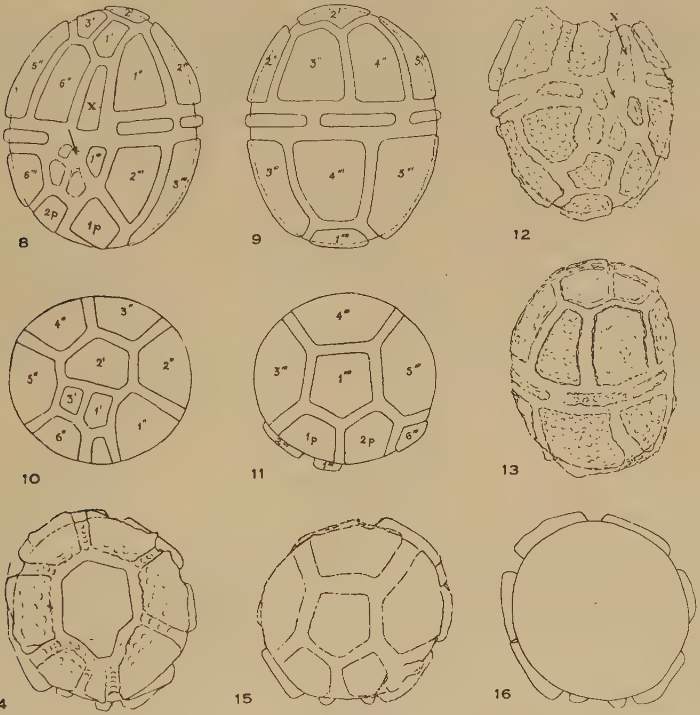
EISENACKIA CRASSITABULATA sp. nov.

Figs. 6-16; Plate 5, Fig. 2

Paleocene to Lower Eocene: Pebble Point Formation, Vic.

Lower Eocene: Princetown Member of the Dilwyn Clay, Vic. (very rare).

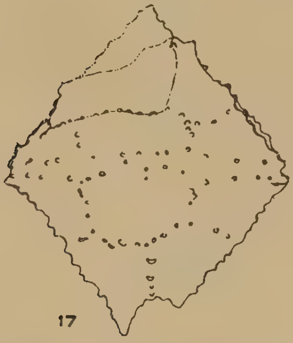
Theca with a relatively thick wall, ellipsoidal, slightly compressed. Epitheca and hypotheca about equal. Transverse girdle level with the surface, slightly but clearly helicoidal. Longitudinal furrow level with the surface indicated on the epitheca by an elongated plate, and on the hypotheca by an inconspicuous and short ventral area. All the plates, including those constituting an equatorial belt corresponding to the girdle, are clearly outlined by a translucent, widely reticulate thickening. At the level of the belt, the girdle is marked not by a single depression but, on the contrary, by a medium elevation with a depression on both sides of it situated between it and the pre-equatorial and post-equatorial plates. All the spaces between the plates, and between the plates and the girdle, are ornamented with a linear thick-walled mesh of the same shape as the plates. In our material, treated as previously indicated and stained with safranin, the thick membrane is strongly coloured red, whilst the raised walls of the reticulum are either pink or uncoloured. Thus, in spite of



Figs. 8-16.—*Eisenackia* gen. nov. *crassitabulata* sp. nov. Fig. 8.—Ventral view of the theca. Fig. 9.—Dorsal. Fig. 10.—Epitheca. Fig. 11.—Hypotheca (schematic). Fig. 12.—A specimen in ventral view, apex broken. Fig. 13.—Oblique apical view of a complete specimen. Figs. 14-16.—The same specimen, epitheca (Fig. 14), hypotheca (Fig. 15), and optical section (Fig. 16) at the level of the equatorial plates. Pebble Point, Vic. × 415.

reservations necessary on account of the age and treatment of the material, there seems to be a certain difference in composition between the 2 parts of the area, i.e. the thick basal membrane and superficial ornamentation.

The schematic tabulation (Figs. 8-11) has been obtained from the examination of some 20 specimens of which, however, only 2 have been complete. All the others have a large apical opening (Fig. 14) that corresponds with few exceptions to the position of the apical plates. These seem to have been interdependent and shed as a whole from the theca, but, since all the specimens in an apical position have lost their apical plates, it has not been possible to determine their exact form and disposition. For this reason, therefore, the number 2-3′ has been given in the generic description. It appears evident that, in this species, the opening formed by the detachment of the apical plates is related to some biological process either associated with the reproduction of the cell by divisions beneath the membrane, or with the exit of a cell after an encystment. In the latter eventuality there will not be a distinct cyst membrane, as is observed in many dinoflagellates, for example, *Deflandrea*, which is present in the same deposit.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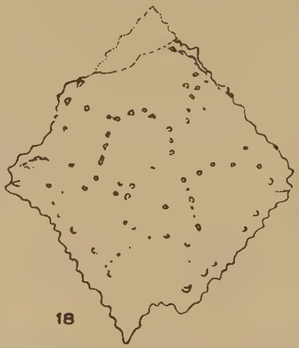
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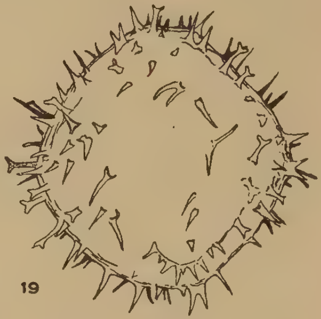
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Figs. 17-18.—*Wetzeliella lineidentata* sp. nov. Surface of the membrane (upper and lower face) of the specimen shown in Plate 5, Fig. 5 (the cyst is not shown). Denmark, W.A. × 346. Fig. 19.—*Wetzeliella homomorpha* sp. nov. (type photographed in Plate 5, Fig. 7). Princetown Member of Dilwyn Clay, Vic. × 552.

In addition to the apical plates just mentioned, the epitheca is composed of 6 pre-equatorial plates. One plate (x on Figs. 8 and 12) occupies the position of the upper longitudinal furrow. This plate can be compared with the more or less diamond-shaped 1st apical plate characteristic of the genus *Peridinium*. However, the general affinities of the genus *Eisenackia* do not approach the genus *Peridinium*, where an apical pore, absent in *Eisenackia*, is always found. Also it is more logical to consider plate x as representing the upper part of the longitudinal furrow. The pre-equatorial plates are unequal in size, plates 1″ and 6″ being clearly smaller than the others.

The hypotheca has been intact in all the specimens. It is composed of 6 post-equatorial plates, 1 antapical and 2 posterior intercalaries. The 1st post-equatorial plate 1‴ is very small, and should be considered as 1 of the plates of the ventral area. This reduction of the 1st post-equatorial plate is not unusual in dinoflagellates and, generally speaking, our specimens show this plate more clearly than the others comprising the ventral area.

The antapical plate 1⁗ is always pentagonal, and the 2 sides of the angle directed towards the ventral area are adjacent to the 2 small posterior intercalary plates 1*p* and 2*p*. The ventral area is relatively large and in favourable specimens it is possible to recognize 3 distinct plates and a possible 4th (dotted and indicated by a small arrow in Figs. 8 and 12).

Dimensions.—Relatively constant; length 72-78 μ, breadth 55-67 μ, depth 50-61 μ. A single thicker and more globular specimen differs from all the others, the length being 67 μ and the breadth 58 μ.

The affinities of the genus *Eisenackia* are uncertain. In the flattened nature of the transverse furrow the new genus approaches the Podalampidae, especially the genus *Blepharocysta.* At first sight *Eisenackia crassitabulata* resembles *B. striata* Schütt 1895, but this resemblance is quite superficial, for in the Podolampidae the shell either terminates in a horn-like process or there is an apical pore.

E. crassitabulata to some extent approaches the Protoceratidae, and more precisely the genus *Protoceratium* Bergh., in which there is no apical pore and the ornamentation is in the form of a thick-walled, wide-meshed reticulum. The tabulation of *Protoceratium* is 1-3′, 0*a*, 6″, 0-1*p*, 1-3⁗. The variations indicated by various authors allow us to consider the tabulation of *Eisenackia* as coming within the limits of these variations. The fundamental difference between the 2 genera lies in the absence of a depressed furrow in *Eisenackia.* In the present state of our knowledge of the Dinoflagellata this character appears to be important, and to justify the creation of a new genus and perhaps a distinct family.

Genus DINOPTERYGIUM Deflandre

DINOPTERYGIUM CLADOIDES Deflandre

Plate 1, Fig. 2

Dinopterygium cladoides Deflandre, 1935, Bull. Biol. 69: 231, pl. 8, fig. 6.

Lower Cretaceous: Onepah Station, N.S.W.

Although this curious dinoflagellate is probably not rare, it has hitherto only been described from laterally placed examples in the Upper Senonian flints of France (Deflandre 1936).

The Australian specimen provides a polar view, and enables us to recognize in the microphotograph on Plate 19, Figure 11, of Reissinger (1950) another example of *D. cladoides,* this time from a Belgian Eocene clay.

Thus, in Europe *D. cladoides* has a definitely known stratigraphical range from Upper Senonian to Lower Eocene (Ypresian). If the Lower Cretaceous age of the sample from Onepah Station is confirmed, this organism made a still earlier appearance in the southern hemisphere. A more complete study of this form will ultimately be published.

Types.—Holotype: G. Deflandre, Paris, AF55.

INCERTAE SEDIS

Genus SCHEMATOPHORA gen. nov.

Shell globular, the surface marked into relatively widely spaced polygonal or rounded areas; outlines of the fields delimited by wing-like ridges which become thinner distally. Fields about 15-18 in number; several fields smaller than the others are grouped in a particular region.

Genotype, *Schematophora speciosa* sp. nov.

SCHEMATOPHORA SPECIOSA sp. nov.

Plate 6, Figs. 11-13; Plate 7, Fig. 11

? Lower Eocene: Birregurra, Vic., bore No. 1 at 783-784, 842-843, and 876-877 ft.

? Middle Eocene: Anglesea, Vic.

Miocene or older: Birregurra, Vic., bore No. 1 at 514-516 ft.

Shell ellipsoidal or ovoidal, wing-like ridges with an entire, or more often slightly crenulate, margin, sometimes showing small, clearly defined, vertically placed capitate processes. Bases of ridges irregularly thickened forming small knobs or meshes raised above the more or less clearly marked sculpture of the shell membrane. Any breaks in incomplete shells follow the outlines of the fields, and demonstrate the existence of weaker lines, sometimes distinctly visible, in the spaces between them.

Ridges delimiting the fields sometimes joined by short, transverse bars, especially in the region of the small fields. Fields probably about 16 or 17, amongst which 7-9 are larger and 4-5 small. The small fields are situated in a depressed region which may be considered as the ventral portion. The arrangement of certain of the large quadrangular fields gives the appearance of an incomplete transverse furrow.

Dimensions.—Holotype 54 by 51 μ; range 54-61 μ by 46-54 μ.

The specimens upon which the species *S. speciosa* has been based came from the Birregurra bore between 514 and 877 ft. It does not appear to have been a rare type since, from the relatively small amount of matrix treated, 12 more or less complete examples have been isolated. So far only 1 specimen has been found in the Anglesea sandstone. However, in spite of the number of individuals available, more and better preserved examples are needed to establish the exact tabulation necessary for recognition of the affinities and systematic position of *Schematophora*.

The arrangement of the ornament and general aspect of this organism has been observed for a long time in some microfossils of the Cretaceous flints of France (Deflandre, unpublished data). These microfossils generally show a clear equatorial differentiation which recalls the dinoflagellates, and it is this fact that has led to the provisional position given here to *Schematophora*.

The possibility of an approach to certain types of the Hystrichosphaeridae, for example, *Hystrichosphaera* and *Areoligera*, must not be excluded. The lines of weakness between the fields in *Schematophora* exist also in *Areoligera* (Deflandre, unpublished data) as well as in certain species of *Hystrichosphaeridium* (Deflandre 1937; Lejeune-Carpentier 1940).

Order HYSTRICHOSPHAERIDEA

Family HYSTRICHOSPHAERIDAE

Genus HYSTRICHOSPHAERA O. Wetzel emend. Deflandre

HYSTRICHOSPHAERA FURCATA (Ehrenberg) O. Wetzel

Plate 8, Fig. 9

Xanthidium furcatum Ehrenberg, 1838, Abh. preuss. Akad. Wiss. 1838: 109-36, pl. 1, fig. 14.

Hystrichosphaera furcata (Ehr.) O. Wetzel, 1933, Palaeontographica A 78: 34, pl. 2, fig. 35; pl. 5, figs. 1, 9, 15, and 16.

Lower Cretaceous: Onepah Station, N.S.W.

Lower Eocene: Princetown Member of Dilwyn Clay, Vic.

? Lower Eocene: Birregurra, Vic., bore No. 1 at 833-834 ft, and Nelson Bore, Vic., at 992 ft.

Middle Miocene: Balcombe Bay, Vic.

Only about half a dozen well-characterized examples of this species exist in our material so that, so far as can be judged at present, *H. furcata* at least in its typical form seems to be scarce in Australian deposits and especially in the Cretaceous. This is perhaps surprising, as it is well known to be one of the commonest types in European Senonian flints and also occurs in the Lower Cretaceous (Comanche series) of Texas.

Should the apparent rarity of *H. furcata* (and also *H. ramosa* (Ehr.) O. Wetzel) in the Cretaceous sediments of Australia be confirmed by later work it would have a definite significance. However, research in this field is only beginning and future data could give a quite different idea of the exact occurrence and frequency of the various species.

HYSTRICHOSPHAERA RAMOSA (Ehrenberg) O. Wetzel

Plate 2, Fig. 1; Plate 5, Fig. 6; Plate 6, Fig. 1

Xanthidium ramosum Ehrenberg, 1838, Abh. preuss. Akad. Wiss. 1838: 109-36, pl. 1, fig. 15, No. 1-5.

Hystrichosphaera ramosa (Ehr.) O. Wetzel, 1933, Palaeontographica A 78: 35, pl. 5, figs. 7, 8, 10-12, 18, and 19.

Upper Cretaceous: Gingin, W.A.

? Lower Eocene: Nelson Bore, Vic., at 992 ft.

? Middle Eocene: Anglesea, Vic.

Miocene or older: Birregurra, Vic., bore No. 1 at 514-516 ft.

The photographed specimen from Gingin (Plate 2, Fig. 1) and the form from Anglesea are clearly of the same type as that figured by Lejeune-Carpentier (1937, Plate 2, Fig. 5). In both deposits the species is rare. In the Miocene deposit at Balcombe Bay specimens similar to the one shown in Plate 6, Figure 1, are relatively numerous. These seem to be rather different from the examples from Gingin and Anglesea, both the processes and their branches being longer and thicker. However, they correspond quite well to the examples of *H. ramosa* in European Cretaceous flints.

HYSTRICHOSPHAERA BULLOIDEA sp. nov.

Plate 5, Figs. 3 and 4

Hystrichosphaera furcata Cookson, 1953, pl. 1, figs. 13 and 14.

Miocene or older: Birregurra, Vic., bore No. 1 at 514-516 ft.

Eocene: Canopus Station, S.A., bore at 548-572 ft.

Middle Miocene: Balcombe Bay, Vic., and Gellibrand Clay, Princetown, Vic.

Shell small, spherical or nearly so, having the general appearance of *Hystrichosphaera furcata* and *H. ramosa.* Outline circular in well-preserved specimens, elliptical or oval when broken. Membrane rather thin and delicate, easily broken and crumpled when, owing to their unnaturally close proximity, the processes seem more numerous than in fully expanded examples. Processes always trifurcate, the 3 branches being widely separated and shortly bifurcate.

Dimensions.—Figured type: overall diameter 59 μ, shell 36 μ. Range: overall diameter 54-64 μ, shell 30-37 μ, processes 10-15 μ.

This small species is common in the Balcombian. It is constant in character. *H. bulloidea* differs from *H. furcata* in general outline, dimensions, and nature of the processes and can be distinguished from *H. ramosa* by its spherical shape, smaller size, and generally more slender processes.

HYSTRICHOSPHAERA HYPERACANTHA sp. nov.

Plate 6, Fig. 7

Middle Miocene: Balcombe Bay, Vic.

Miocene or older: Birregurra, Vic., bore No. 1 at 514-516 ft.

Shell globular, spherical or almost spherical; polygonal fields characteristic of the genus with fine, sometimes almost indistinguishable outlines, the equatorial series recognizable by the alignment of the processes. Stalks of processes long, stiff, often slender, dividing into 3 distinct branches with simple or bifurcate apices, inserted both at the angles of the fields and along their sides, the usual arrangement being 1 process to each angle of the field and 2 along each side.

Dimensions.—Diameter of shell 54-59 μ, overall diameter 92-97 μ, length of processes 13-20 μ.

This new species is apparently close to *H. ramosa* Ehr. (O. Wetzel) sensu lato and *H. setosa* Philipot. *H. hyperacantha* can immediately be distinguished from *H. setosa* by its trifurcate processes. Possibly certain forms previously considered as *H. ramosa* may really belong to *H. hyperacantha*, but the specimens classified by various authors as *H. ramosa* usually have not had intercalary processes between those situated at the angles of the polygonal fields or at the most only one. Moreover the boundaries of the fields are always strongly marked in the group *H. furcata-H. ramosa*. In *H. hyperacantha* they may be so indistinct as to incline one to regard the specimen as a species of *Hystrichosphaeridium*. Perhaps a study of favourable material may ultimately lead to a generic revision of those species of *Hystrichosphaeridium* that have been described from insufficiently well-preserved individuals.

HYSTRICHOSPHAERA CRASSIPELLIS sp. nov.

Fig. 20; Plate 6, Figs. 2 and 3

Lower Eocene: Princetown Member of the Dilwyn Clay, Vic.

? Lower Eocene: Birregurra, Vic., bore No. 1 at 889 and 890 ft.

Shell globular, almost spherical, with an unusually thick membrane; lines separating the fields sometimes rather indistinct, sometimes aliform; fields polygonal, the elongated equatorial series present. Processes apparently fragile, formed of a thin transparent membrane, forked or more or less divided at the apex. Surface of shell membrane ornamented with a clearly marked reticulum, the meshes being about 1.5-2 μ. In certain examples the mesh is finer and closer. The membrane is non-homogeneous and shows a fibrillar structure.

Dimensions.—Diameter of shell *c.* 74-89 μ, overall diameter *c.* 105-117 μ, appendages *c.* 23-26 μ.

None of the described species of *Hystrichosphaera* from the Mesozoic has such a thick shell membrane as *H. crassipellis*. However, one of us (G.D.) has found, not uncommonly but not described, an analogous although specifically different form in the Oligocene of Innien, Germany.

HYSTRICHOSPHAERA SPECIOSA Deflandre

Plate 8, Fig. 10

Hystrichosphaera speciosa Deflandre, 1934, C. R. Acad. Sci., Paris 199: 967, fig. 4.

Lower Cretaceous: Onepah Station, N.S.W.

Paleocene to Lower Eocene: Pebble Point Formation, Vic.

Miocene or older: Birregurra, Vic., bore No. 1 at 514-516 ft.

The specimen from Onepah Station is completely typical. Its dimensions (46 by 38 μ) agree and it possesses the short horn-like polar appendage and reduced processes at the angles of the fields that characterize *H. speciosa*.

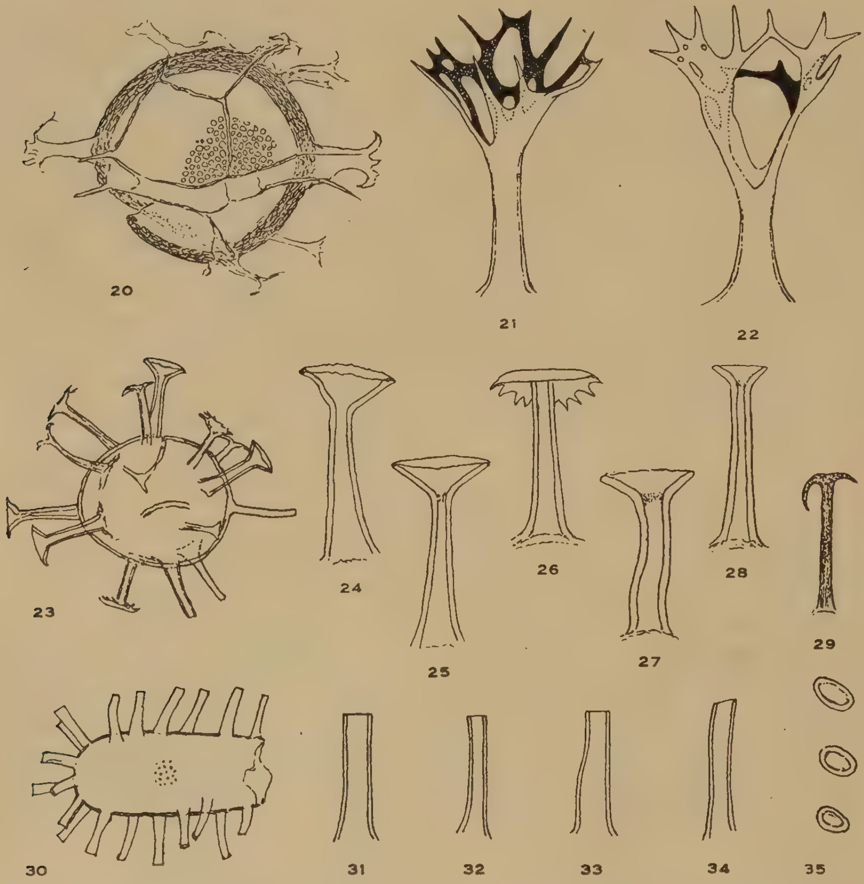


Fig. 20.—*Hystrichosphaera crassipellis* sp. nov. Princetown Member of Dilwyn Clay, Vic. × 390. Figs. 21-22.—*Hystrichosphaeridium pulcherrimum* sp. nov. Two processes from the photographed type, Plate 1, Fig. 8. × 982. Figs. 23-29.—*Hystrichosphaeridium choanophorum* sp. nov. Fig. 23.—Type. × 622. Figs. 24-26.—Three processes of the type. × 1545. Figs. 27-29.—Three processes from a paratype. Hampton, Vic. × 1545. Figs. 30-35.—*Hystrichosphaeridium isocalamus* sp. nov. Type figured in Plate 2, Figs. 7-8. Fig. 30.—Optical section and surface ornamentation. × 390. Figs. 31-34.—Four processes. × 1545. Fig. 35.—Transverse section of processes. Onepah Station, N.S.W. × 1545.

The third example from Birregurra is doubtful; it also possesses the short horn-like polar appendage but lacks the reduced processes at the angles. It could also be referred to *H. cingulata* (O. Wetzel) Defl., but the ribs are not wing-like and the latter species does not possess an apical process.

Types.—Holotype: Coll. G. Deflandre, Paris, AJ1.

HYSTRICHOSPHAERA CINGULATA (O. Wetzel) Deflandre

Plate 6, Figs. 4 and 5

Cymatiosphaera cingulata O. Wetzel, 1933, Palaeontographica A 78: 74, pl. 4, fig. 10.

Hystrichosphaera cingulata (O. Wetzel) G. Deflandre.

? Lower Eocene: Nelson Bore, Vic., at 992 ft.

Middle Eocene: Anglesea, Vic.

Miocene or older: Birregurra, Vic., bore No. 1 at 514-516 ft.

Middle Miocene: Balcombe Bay and Gellibrand Clay, Vic.

Many years ago a set of specimens belonging to this species was found in Senonian flints of the Paris basin (Deflandre, unpublished data), and their exact position in the genus *Hystrichosphaera* was recognized. The present results confirm this opinion.

Specimens similar to those of *H. cingulata* in European Senonian flints have been found in several Australian Tertiary deposits, the only variation from the type being the lower ridges delimiting the fields shown by a few of the examples.

The arrangement of the ridges is that typical of *H. furcata,* the quadrangular equatorial fields and the triangular field figured by one of us (Deflandre 1937, Plate 11, Fig. 4) for *H. furcata* being evident. The ridges themselves are, as in *H. furcata* var. *velata* O. Wetzel, more strongly developed than in *H. furcata* and in the Australian examples range from 3 to 10 μ in height.

H. cingulata also differs from *H. furcata* and allied species in the complete absence of processes. It is distinct from *H. speciosa,* the only species with which the examples with reduced ridges are comparable, in the complete absence of polar appendages.

Dimensions.—Balcombe Bay examples: 53 by 48 μ, 74 by 69 μ, 69 by 69 μ, wing 8-10 μ. Nelson Bore example: overall length 48 by 42 μ, wing 3 μ.

Types.—Holotype: Coll. O. Wetzel, Eutin, No. 133.

HYSTRICHOSPHAERA WETZELI Deflandre

Lower Cretaceous: Onepah Station, N.S.W.

A few individuals belonging to this species were found in the Onepah sample. They possess reduced ribs and processes and the polar prismatic structure that characterizes the holotype. The sides are parallel and the membrane thin and smooth.

For affinities see under *H. borussica* Eis.

HYSTRICHOSPHAERA BORUSSICA Eisenack

Plate 5, Figs. 9 and 10

Hystrichosphaera borussica Eisenack, 1954, Palaeontographica A 105: 62, pl. 9, figs. 5-7.

Middle Miocene: Balcombe Bay and Gellibrand Clay, Vic.

It appears evident that a group of *Hystrichosphaera* comprising *H. borussica* and *H. wetzeli* exists in which the delimitation of each species is as difficult as in the group *H. furcata-H. ramosa.*

The specimen shown in Plate 5, Figure 9, in which the apical part is more like a frustum of a cone or pyramid than a cylinder or straight prism, seems at first sight quite different from the representation of *H. borussica* as given by Eisenack (1954). Other specimens have been observed which are nearer to the type, but at the same time not far from *H. wetzeli.* In the present state of our knowledge we tentatively use the name proposed by Eisenack for Tertiary forms of this character.

Dimensions.—Figured specimen: shell, length 64 μ, breadth 54 μ, overall length 115 μ, overall breadth 79 μ.

Types.—Holotype: A. Eisenack, Reutlingen, Ph. 23.

The badly preserved individual shown in Plate 5, Figure 10, demonstrates the occurrence of this kind of *Hystrichosphaera* or perhaps the related species *H. ovum* Defl. in the Lower Tertiary of Western Australia.

Genus NEMATOSPHAEROPSIS gen. nov.

Shell globular, divided into fields by ridges, an equatorial series developed as in the genus *Hystrichosphaera.* Branches of processes joined to one another by trabeculae or filaments as in the genus *Cannosphaeropsis.*

Genotype, *Nematosphaeropsis balcombiana* sp. nov.

NEMATOSPHAEROPSIS BALCOMBIANA sp. nov.

Plate 8, Fig. 5

Middle Miocene: Gellibrand Clay, Princetown, Vic.

Characters of the genus: shell slightly elliptical, with numerous processes of which the longest approaches half the diameter of the shell. Processes trifurcate, the extremities of the 3 branches joined to neighbouring processes by delicate filaments.

Dimensions.—Diameter of shell *c.* 31 μ, overall diameter 61 by 56 μ, length of processes 13-15 μ.

The dimensions are those of the holotype, which is well preserved. A second example has processes 10-13 μ long but the shell is much shrunken, the total diameter being reduced to about 38 μ.

The genus *Nematosphaeropsis* is as clearly morphologically derived from the genus *Hystrichosphaera* as the genus *Cannosphaeropsis* appears to be from certain species of *Hystrichosphaeridium.*

It may be noted that in another Australian organism described below under the name *Hystrichokibotium trabeculiferum* there is a tendency to develop connected processes, but in this form only some and not all of the processes are joined.

Genus HYSTRICHOKIBOTIUM Klumpp

HYSTRICHOKIBOTIUM TRABECULIFERUM sp. nov.

Plate 8, Fig. 6

Middle Miocene (Balcombian): Balcombe Bay, Vic.

Shell globular, its surface divided by ridges into polygonal fields which do not appear to form a distinct equatorial girdle. The numerous processes arise from the angles of the fields; they are of variable length, simply forked, and in a single individual are both free or connected to one another by filiform or ribbon-like trabeculae.

Dimensions.—Diameter of shell *c.* 32 μ, overall diameter *c.* 59 μ.

This curious species has characters of both the genus *Hystrichokibotium* Klumpp and, in possessing trabeculae connecting the extremities of the processes, of the genus *Cannosphaeropsis* O. Wetzel emend. Deflandre. *H. trabeculiferum,* together with the genus *Nematosphaeropsis,* shows that this type of structure is not exclusively confined to hystrichospheres without polygonal fields.

Genus HYSTRICHOSPHAERIDIUM Deflandre

HYSTRICHOSPHAERIDIUM RECURVATUM (White) Lejeune-Carpentier

Plate 1, Figs. 11 and 12

Xanthidium recurvatum White, (1842) 1844, Trans. Micr. Soc. 1: pl. 8, fig. 11.
Hystrichosphaeridium recurvatum (White) Lejeune-Carpentier, 1940, Ann. Soc. Géol. Belg. 63: B221, fig. 6.

Upper Cretaceous (Senonian): Gingin, W.A.

Lejeune-Carpentier (1940) in a precise review of *H. recurvatum* has given the number of processes per shell as about 30. Our specimen from Gingin in possessing 28 appendages, and the *H. tubiferum* of Deflandre (1937, Plate 13, Fig. 4), which Lejeune-Carpentier has recognized as *H. recurvatum,* in possessing 29, correspond perfectly to the limits fixed by the Belgian author.

Dimensions.—Figured specimen: overall diameter *c.* 90 μ, shell 51 by 44 μ, appendages 18-26 μ long and *c.* 3 μ wide.

Types.—Plesiotype: Coll. Lejeune-Carpentier, Liège, CXII, 17.

Less certain is the identity of a series of specimens (Plate 1, Fig. 12) having the general features of *H. recurvatum* that occurs in the Lower Cretaceous deposit at Onepah Station. All are well beyond the lower limits of *H. recurvatum* as described by Lejeune-Carpentier. The shells are smaller and the appendages shorter, finer, and considerably more numerous (37-43) than in typical examples of *H. recurvatum*. In spite of these differences, however, it seems better for the present to include these specimens in *H. recurvatum* rather than to create a new species for their reception. It may be noted that the tubular character of the appendages has been difficult to determine, perhaps owing to the method of isolation and staining employed.

Dimensions.—Overall diameter 64-69 μ, diameter of shell 36-41 by 31-36 μ, appendages 10-18 μ long and *c.* 1.5 μ wide.

HYSTRICHOSPHAERIDIUM COMPLEX (White) Deflandre

Plate 1, Figs. 9 and 10

Xanthidium tubiferum complex White, 1842, Micr. J. 2: pl. 4 (3), fig. 11; (1842) 1844, Trans. Micr. Soc. 1: 83, pl. 8, fig. 10.

Hystrichosphaeridium elegantulum Lejeune-Carpentier, 1940, Ann. Soc. Géol. Belg. 63: B222, figs. 11-12.

Hystrichosphaeridium complex (White) Deflandre, 1946, C.R. Soc. Géol. Fr.: 111.

H. cf. *tubiferum* sec. Cookson 1953, pl. 2, fig. 24.

Lower Cretaceous: Onepah Station, N.S.W.

Upper Cretaceous (Senonian): Gingin, W.A.

? Upper Cretaceous: Nelson Bore, Vic., at 5782 and 6192 ft.

This species is taken in a rather broader sense than that admitted by Lejeune-Carpentier (1940). In addition to having appendages with extremities identical with those figured by this author, some of the Australian specimens referred to *H. complex* have a variable number of processes which are slightly clathrate and more like those of *H. pulcherrimum* (described below). However, the holes in the walls of the terminal expansions are extremely small and few in number, and the funnels are not so deep as they are in *H. pulcherrimum*.

Dimensions.—Overall diameter 92-102 μ, diameter of shell 36-55 μ by 36-51 μ, length of appendages 20-33 μ, number of processes less than 20.

Types.—Plesiotype: Coll. Lejeune-Carpentier, Liège, CVIII, 4.

HYSTRICHOSPHAERIDIUM PULCHERRIMUM sp. nov.

Figs. 21 and 22; Plate 1, Fig. 8

Lower Cretaceous: Onepah Station, N.S.W.

Shell ellipsoidal, with about 14 appendages, the longest of which are generally shorter than the diameter of the shell. At about half their length the appendages gradually widen into deep, strongly perforated funnels, the walls of which are almost reticulate. The rims of the funnels are fringed with numerous spines which may be connected by small threads.

Dimensions.—Holotype: overall diameter *c.* 118 μ, shell 47 by *c.* 61 μ, appendages 26-38 μ.

This species is allied to *H. complex* (White) Defl. from English Upper Senonian flints in which processes with slightly perforated funnels sometimes occur. It seems probable that *H. pulcherrimum* represents one of the stages in an evolutionary series that led from *Hystrichosphaeridium* to the genus *Cannosphaeropsis*. *C. aemula* Defl., for example, has very similar appendages to those of *H. pulcherrimum*, the main distinction between the 2 species being the existence in *C. aemula* of connecting threads between neighbouring processes.

HYSTRICHOSPHAERIDIUM SALPINGOPHORUM Deflandre

Plate 2, Fig. 9

Hystrichosphaera salphingophora Deflandre, 1935, Bull. Biol. 69: 232, pl. 9, fig. 1.
Hystrichosphaeridium salpingophorum Deflandre, 1937, Ann. Paléont. 26: 22, pl. 13, figs. 1 and 3.

Lower Cretaceous: Era River, Papua, New Guinea.

The figured specimen, although considerably damaged, possesses at least 1 process (lower right-hand) with the distal quadrangular opening typical of this species.

The rarity of this type in the Australian collection is a noticeable fact. *H. salpingophorum* is known from the Jurassic (Oxfordian) and Cretaceous of Europe. It is interesting to find it in New Guinea in association with *Cannosphaeropsis aemula* Defl., which also occurs in the Oxfordian, but which still has not been found in European Cretaceous deposits.

Types.—Holotype: Coll. G. Deflandre, Paris, AJ56.

HYSTRICHOSPHAERIDIUM CHOANOPHORUM sp. nov.

Figs. 23-29

Post-Upper Miocene (post-Cheltenhamian): Hampton, Vic.

Shell globular, furnished with tubular processes not communicating with the interior. Processes cylindrico-conical, abruptly widened into a small funnel with a rough margin, sometimes into a flat expansion with a finely denticulate margin or, rarely, terminated by 2 recurved spine-like outgrowths. Membrane smooth or indistinctly granular.

Dimensions.—Shell 30-34 μ, processes 15-17 μ long, overall diameter 54-63 μ.

The type of process having funnel-shaped terminations with almost smooth margins is at present known only in 1 species, namely, *Hystrichosphaeridium simplex* (White) Defl., found by White in English Senonian flints. *H. simplex*, which as yet has not been rediscovered, is considerably larger (*c.* 100 μ overall) than *H. choanophorum*.

Our 2 specimens possess both funnel-like processes and others that recall the process of *Hystrichosphaeridium tubiferum* sensu lato of the

European Cretaceous flints. It must be remembered, however, that in *H. tubiferum* the bases of the processes are open so that the inner cavity of the shell is in direct communication, through the processes, with the exterior, whereas in *H. choanophorum* the bases are closed.

HYSTRICHOSPHAERIDIUM ISOCALAMUS sp. nov.

Figs. 30-35; Plate 2, Figs. 7 and 8

Lower Cretaceous: Onepah Station, N.S.W.

Shell elongate-elliptical, covered by a large number of tubular processes with cleanly truncate apices, tubes of equal length, and elliptical cross section, possibly communicating with the interior. Surface of shell punctulate.

Dimensions.—Holotype (incomplete): overall length 67 μ, breadth 38 μ, shell 42 μ long and 18 μ broad, tubes 10-11 μ long.

The interest of this new species lies in the shape of the shell, elongate-elliptical forms being rare amongst hystrichosphaerids. In this respect it approaches *H. xanthopyxides* (O. Wetzel) Defl. of European Cretaceous flints. However, the short truncated tubes of *H. isocalamus* are quite distinct from the long pointed horns of *H. xanthopyxides* and its variety *granulosum.*

HYSTRICHOSPHAERIDIUM POLYTRICHUM Valensi

Plate 2, Fig. 2

Hystrichosphaeridium polytrichum Valensi, 1947, C. R. Acad. Sci., Paris 225: 818, fig. 4.

Upper Cretaceous (Senonian): Gingin, W.A.

The Australian form has been compared with the type specimen of *H. polytrichum* of the French Jurassic flints and appears to differ from it only in details that may be due to the method of preparation. The general dimensions and the density and length of the long, pointed processes are very similar. These characters, however, are found in several species of *Hystrichosphaeridium* which are very difficult to distinguish clearly from one another. This group, which includes *H. pseudhystrichodinium* Defl. sensu lato, *H. spinosum* (White) Defl., *H. palmatum* Defl. & Court, *H. polytrichum* Val., *H. hirsutum* (Ehr.) Defl. (pars), perhaps *H. striolatum* Defl. sensu lato, and also *Hystrichosphaeridium* sp. (= *Xanthidium furcatum*; see White 1842), needs to be completely revised.

Types.—Holotype: Coll. G. Deflandre, Paris, BS38.

HYSTRICHOSPHAERIDIUM CENTROCARPUM sp. nov.

Plate 8, Figs. 3 and 4

Hystrichosphaeridium sp. *a* Cookson, 1953, p. 115 and pl. 2, figs. 26 and 27.

Miocene or older: Birregurra, Vic., bore No. 1 at 514-516 ft.

Middle Miocene (Balcombian): Balcombe Bay and Gellibrand Clays, Vic.

Shell globular, more or less ellipsoidal (probably by deformation), covered with numerous straight, slender processes placed irregularly or with a certain alignment. Processes solid, showing radiating fibrils at their point of insertion on the shell, which is clearly ornamented with a fine reticulum. The slightly widened apices of the processes are fringed with 10 or more small curved spines (this structure is only visible with a high-powered objective).

Dimensions.—Diameter of shell 54-80 μ, length of processes 13-18 μ, total diameter *c.* 97-115 μ.

As a result of the relative thinness of the shell membrane none of the specimens has been completely intact. Most of the examples have a large irregular or more or less angular opening.

H. centrocarpum, in spite of its generally similar appearance, does not belong to the species group of *Hystrichosphaeridium multifurcatum* Defl.-*H. major* Lej.-Carp. known from the European Cretaceous flints. In these species the hollow processes have a quite different structure.

HYSTRICHOSPHAERIDIUM FIMBRIATUM (White) Deflandre

Plate 2, Fig. 4

Xanthidium fimbriatum White, 1842, Micr. J. 2: pl. 4 (3), fig. 3; (1842) 1844, Trans. Micr. Soc. 1: pl. 8, fig. 2.

Hystrichosphaeridium fimbriatum (White) Deflandre, 1946, in Deflandre and Deflandre-Rigaud, Fichier Micropaléontologique, Sér. 8: 899.

Lower Cretaceous: Onepah Station, N.S.W.

Shell globular, spherical or ellipsoidal, completely covered with very numerous, short processes of equal length with capitate or furcate apices giving the appearance of continuity between them.

Dimensions.—Shell 26-38 μ, appendages *c.* 3-4 μ, overall diameter 31-46 by 31-41 μ.

The dimensions given by White for *Xanthidium fimbriatum* are 51-77 μ (1/500 to 1/300 in.), but although mentioning that the processes were too numerous to count, White gave no information regarding the detailed appearance of the processes. Up to the present White's species has not been cited by writers on the microfossils of European deposits. The Australian form taken as a new type of *H. fimbriatum,* although considerably smaller than the original specimens, exactly corresponds in appearance to the first figure of White (1844, Plate 4 (3), Fig. 3) in which the enlarged extremities of the processes can be clearly seen. In White's second figure (1844, Plate 8, Fig. 2) of the same species the frequently recurved processes have pointed or blunt, but not enlarged apices. This example may be another species or simply a form of *Hystrichosphaeridium whitei* Defl. & Court.

H. fimbriatum in its typical form is easily recognizable. However, another organism exists in the Onepah deposit (Plate 7, Fig. 12) with which it may be confused. The body of this organism (overall measurement between 40 and 45 μ), which sometimes has a somewhat angular outline recalling that of certain dinoflagellates, is covered with numerous short forked processes, the branches of which lie close together and seem to be covered with a delicate finely granular external membrane. This organism cannot be placed in any of the known genera, so until more information about it can be obtained it seems better to leave it unnamed.

HYSTRICHOSPHAERIDIUM MACHAEROPHORUM sp. nov.

Plate 9, Figs. 4 and 8

Miocene or older: Birregurra, Vic., bore No. 1 at 514-516 ft.

Middle Miocene: Balcombe Bay and Gellibrand Clay, Vic.

Shell globular, subspherical or ellipsoidal with a rigid membrane, more brittle than deformable, covered with numerous long, stiff, conical, pointed processes resembling the blade of a dagger. Surface of shell granular or punctate.

Dimensions.—Diameter of shell 41-54 μ, length of spines 13-18 μ, overall diameter 64-74 μ.

The figured type represents an average form as regards the number of processes and their density. Examples with more widely spaced processes are rare; on the contrary specimens with more numerous and more densely arranged spines are relatively frequent.

Generally most of the spines are stiff but sometimes they are somewhat flexible and recurved. The apices are very sharply pointed and often twisted in specimens mounted in Canada balsam.

This species belongs to the type of *Hystrichosphaeridium* of which representatives have already been recorded from Silurian and Cretaceous deposits and which are usually assigned to *H. hirsutum* (Ehr.) and its varieties and forms or to *H. hirsutoides* Eis. One of us has shown (Deflandre 1946) that the name *H. hirsutum* cannot be retained because it corresponds exactly to *Xanthidium hirsutum* which in reality is a desmid (*Staurastrum hirsutum* (Ehr.) Ralfs.).

A general revision of this group of hystrichospheres is badly needed.

HYSTRICHOSPHAERIDIUM FLOSCULUS Deflandre

Plate 2, Fig. 3

Hystrichosphaeridium flosculus Deflandre, 1937, Ann. Paléont. 26: 27, pl. 15, figs. 5 and 6.

Upper Cretaceous (Senonian): Gingin, W.A.

The dimensions and nature of the appendages of the few examples of this species observed are analogous to those specimens in Cretaceous flints of France.

Dimensions.—Diameter of shell *c.* 38 μ, overall diameter 61-69 μ.

Types.—Holotype: Coll. G. Deflandre, Paris, AF46.

HYSTRICHOSPHAERIDIUM STRIATOCONUS sp. nov.

Fig. 36; Plate 2, Fig. 10

Upper Cretaceous (Senonian): Gingin, W.A.

Shell rather robust and thick-walled, globular to spheroidal, ornamented with about 20 bluntly pointed conical processes, the apex of which is normally closed but is frequently broken off leaving a direct opening into the process. Each cone is provided with a number of strong ribs that are thicker at the base and taper towards but do not reach the apex; some of the ribs extend to about half the height of the cone, others stop 3-4 μ from the summit. The shell generally has a polygonal or rounded opening. Surface of shell smooth.

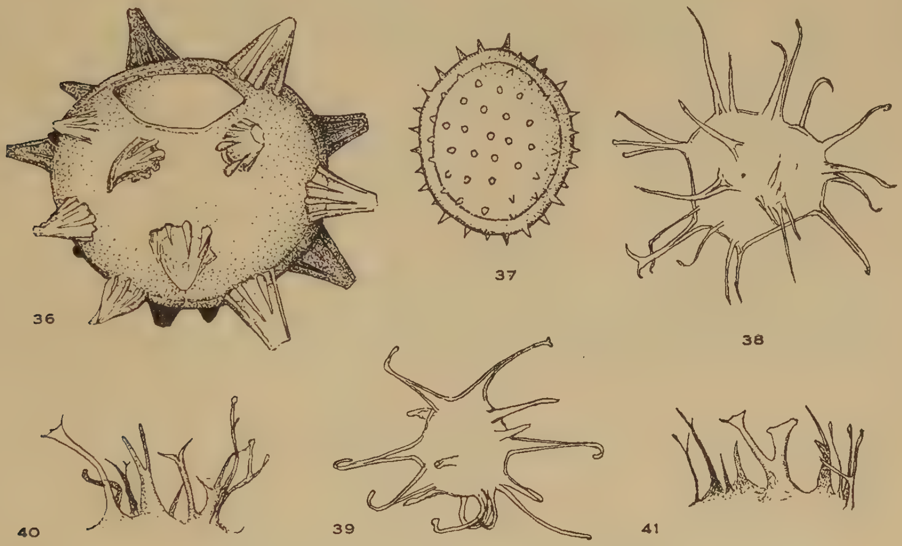


Fig. 36.—*Hystrichosphaeridium striatoconus* sp. nov. Holotype. P16227. Gingin, W.A. × 622. Fig. 37.—*Micrhystridium pachydermum* sp. nov. Holotype. Onepah Station, N.S.W. × 1545. Figs. 38-39.—*Micrhystridium* cf. *stellatum* Defl. Pebble Point, Vic. × 982. Figs. 40-41.—*Hystrichosphaeridium heteracanthum* sp. nov. Two groups of processes. Nelson Bore, Vic. × 622.

Dimensions.—Shell alone 52-57 μ, cones 12-18 μ long.

At the base of each cone a distinct circular line corresponding to the interior wall of the cone (the exterior contour is strongly indented by the ribs) can be seen, but it has not been possible to decide from the present preparations whether or not the cones communicate with the interior of the shell. All the specimens have become strongly coloured by the safranin in the mounting medium and show neither a clear interruption nor a thinning of the shell in the region of the cones.

H. striatoconus is relatively abundant in the Lower Greensand at Gingin; it is distinctly different from all known species of *Hystrichosphaeridium.*

HYSTRICHOSPHAERIDIUM FLORIPES sp. nov.

Plate 7, Figs. 1, 2, and 7

Probably Lower Tertiary: near Denmark, W.A.

Shell globular, with about 16-18 tubular processes not communicating with the interior. Processes generally consisting of from 2 to several tubes joined along the greater part of their length, the individual tubes widening and sometimes separating from one another distally. Proximally the peripheral tubes widen considerably as they fuse with the membrane of the shell, forming on its surface a clearly defined flower-like design. Sometimes the processes may consist of a single tube with a rounded base. Membrane of shell thin and finely reticulate.

Dimensions.—Shell *c.* 45-72 μ by 32-59 μ, processes 20-46 μ long and 3-28 μ wide.

None of the specimens is perfectly preserved; the number of processes as well as the dimensions of the shell must therefore be considered as only approximate. *H. floripes* is a very clearly defined species, easy to recognize and quite distinct from any other known form.

HYSTRICHOSPHAERIDIUM HETERACANTHUM sp. nov.

Figs. 40 and 41; Plate 2, Figs. 5 and 6

Upper Cretaceous (Senonian): Gingin, W.A.

? Upper Cretaceous: Nelson Bore, Vic., at 5782-6192 ft.

Paleocene to Lower Eocene: Pebble Point Formation, Vic.

? Paleocene to Lower Eocene: Nelson Bore, Vic., at 3874 ft.

Shell large, approximately circular in outline, with numerous appendages of variable shape, size, and form. Appendages solid, usually elongated, frequently filiform, sometimes (Plate 2, Fig. 6) as broad as long, the apices either pointed, everted, or irregularly branched. Surface of shell punctate.

Dimensions.—Shell 56-107 μ, appendages 5-36 μ long (majority between 13 and 23 μ).

HYSTRICHOSPHAERIDIUM PLACACANTHUM sp. nov.

Plate 9, Figs. 1-3

Miocene or older: Birregurra, Vic., bore No. 1 at 514-516 ft.

Middle Miocene (Balcombian): Balcombe Bay and Gellibrand Clay, Vic.

Shell globular, circular or asymmetrical in outline, with a large number of processes that are aligned so as to divide the whole surface into more or less polygonal plate-like areas or fields. Each field is separated from its neighbours by an area devoid of appendages. Processes solid, of variable form, somewhat flexuous, simple or branched with pointed or hammer-shaped extremities, widening at the base. Sometimes the bases of 2 or more processes are connected by bridge-like strands; occasionally the apices may coalesce or be connected by a delicate thread as in *Cannosphaeropsis*.

The fields seem to be of variable size and to have no special equatorial arrangement. The surface of the shell is finely reticulate.

Dimensions.—Holotype: shell 64 by 54 μ, overall 105 by 82 μ. Other examples: overall diameter 79-96 μ, diameter of shell 49-54 μ, appendages 18-31 μ long.

The many specimens examined have all been incomplete, a break in the shell being situated in the perhaps accidentally flattened region of the shell. It is this flattening that gives the asymmetrical appearance of those individuals viewed laterally.

An attempt has been made to associate *H. placacanthum* with *Areoligera* Lej.-Carp., but in no example has there been observed the large area free of processes that characterizes this genus. *H. placacanthum* is considered a variable species and it seems possible that later studies may result in the separation of certain exceptional forms, for example, those possessing transverse trabeculae.

H. placacanthum is especially abundant in the Gellibrand Clay (Balcombian) of western Victoria.

HYSTRICHOSPHAERIDIUM INODES Klumpp

Plate 8, Fig. 7

Hystrichosphaeridium truncigerum Cookson, 1953, p. 114, pl. 2, figs. 21-23, non *H. truncigerum* Defl.

Hystrichosphaeridium inodes Klumpp, 1953, Palaeontographica A 103: 391, pl. 18, figs. 1, 2.

Lower Eocene: Princetown Member of Dilwyn Clay, Vic.

? Lower Eocene: Birregurra, Vic., bore No. 1 at 760-761 and 959-960 ft.

Upper Eocene or older: Castle Cove, Vic.

Eocene: Canopus Station, S.A., at 920-925 ft.

This globular species is well characterized by the 2-layered shell membrane, which consists of an outer delicate fibrillar layer, very clearly shown in coloured specimens, which gives rise to the processes, and a rather thicker, more homogeneous inner layer better seen in uncoloured individuals.

As already stated (Cookson 1953) the walls of the appendages are traversed by slender fibrils which run from apex to base, at which point they radiate onto the outer part of the shell membrane. In the Australian as in the European forms the processes are of variable size; however, comparison of the topotypes in the collection of the Laboratoire de Micropaléontologie, Paris, shows that individuals with wide processes are more rare in the Upper Eocene of Germany studied by Klumpp (Bore Wöhrden). On the contrary, in the examples met with at the Australian localities the large processes have been in the majority, and *H. inodes* subsp. *gracilis* Eis., in which all the processes are narrow, has not been met with.

HYSTRICHOSPHAERIDIUM cf. TIARA Klumpp

Plate 7, Fig. 13

Hystrichosphaeridium tiara Klumpp, 1953, Palaeontographica A 103: 390, pl. 17, figs. 8-10.

Hystrichosphaeridium sp. *b* Cookson, 1953, p. 115, pl. 2, fig. 28.

? Middle Eocene: Anglesea, Vic.

Miocene or older: Birregurra, Vic., bore No. 1 at 514-516 ft.

Shell globular with numerous thin, smooth, solid processes capitate or furcate at the extremity. Membrane rather thick with a coarsely granular or irregularly reticulate surface. Polar aperture relatively large, preformed, opened by the splitting off of a cap-like region (actually observed in the figured specimen).

Dimensions.—Figured specimen: diameter of shell 44 by 58 μ, size of opening 33 by 34 μ, length of processes 10-23 μ.

This species recalls *H. tiara* Klumpp but differs from it: (i) in the thickness of the membrane, which is only about 2 μ instead of 4 μ; (ii) in the sculpture of the membrane, which is more granular than filamentous and the internal smooth layer less distinct; (iii) by the absence of a collarette at the base of the processes which appears to be derived from the internal layer. This last point needs verification because the coloration with safranin makes the examination of this structure difficult.

HYSTRICHOSPHAERIDIUM COLLIGERUM sp. nov.

Plate 7, Fig. 3

Hystrichosphaeridium sp. *c*. Cookson, 1953, pl. 2, figs. 29 and 30.

Lower Eocene: Princetown Member of Dilwyn Clay, Vic.

Shell globular, almost spherical; processes numerous, tubular, straight or slightly flexuous, with a conical base and a closed capitate or slightly furcate apex. At 1 pole of the shell there is a large, hollow, cylindro-conical outgrowth closed by a rounded conical apex. This outgrowth, like the small processes, does not communicate with the interior of the shell. It is frequently ornamented distally with a circle of short, blunt, hollow, conical knobs. Membrane of shell finely granular.

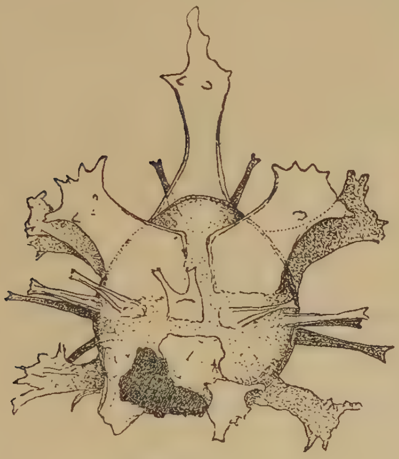
Dimensions.—Holotype: diameter of shell 33 μ, overall diameter 56 μ, large process 20 by 13 μ, small processes *c.* 13 μ long. Range: shell 30-33 μ, overall diameter 56-59 μ, appendages *c.* 13 μ.

Genus HYSTRICHOKOLPOMA Klumpp

HYSTRICHOKOLPOMA RIGAUDAE sp. nov.

Fig. 42; Plate 6, Figs. 6 and 10

Lower Eocene: Princetown Member of Dilwyn Clay, Vic.
? Lower Eocene: Birregurra, Vic., bore No. 1 at 760-843 ft.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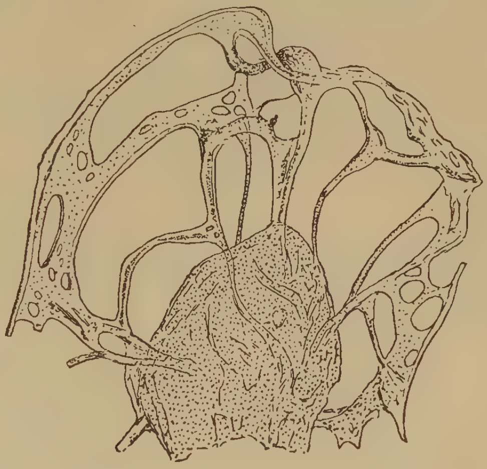
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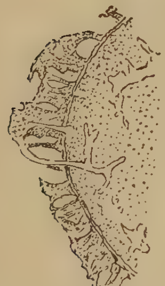
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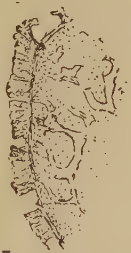
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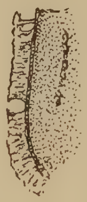
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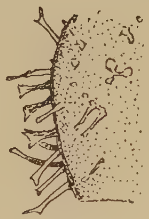
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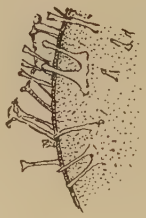
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Fig. 42.—*Hystrichokolpoma rigaudae* sp. nov. Birregurra, Vic. × 622. Fig. 43.—*Cannosphaeropsis fenestrata* sp. nov. Gingin, W.A. × 622. Figs. 44-46.—*Cyclonephelium* gen. nov. *compactum* sp. nov. Groups of processes. × 622. Figs. 44-45.—Onepah Station, N.S.W. Fig. 46.—Gingin, W.A. Figs. 47-48.—*Cyclonephelium distinctum* sp. nov. Groups of processes. Gingin, W.A. × 622.

? Middle Eocene: Anglesea, Vic.
Eocene: Canopus Station, S.A., bore at 548-572 ft.
Miocene or older: Birregurra, Vic., bore No. 1 at 444-449 and 514-516 ft.

Shell globular, more or less ellipsoidal, with approximately axial symmetry and processes of 2 kinds not communicating with the interior, disposed in parallel series starting from 1 pole considered as apical. Antapical pole with a large aperture having a straight or angular margin. Bases of the large processes marked by lines forming quadrangular areas that give the impression of plates. Large processes always closed at their distal extremities, generally widened and provided with more or less numerous and sometimes relatively long horns. The large process situated at the apical pole is often longer than the others and is sometimes prolonged into a hollow horn.

The narrow tubular processes are slightly widened or divided at their extremities, which are either open or closed. Certain filiform processes seem to be solid throughout.

The narrow processes forming the equatorial series are about 10 in number, of which some may be paired. Between the equatorial series and the apex there is a circle of 4 large appendages and a space occupied by a small number (3-5) of narrow processes similar to those of the equatorial belt.

Below the equator there is a circle of 6 large processes, or in certain specimens 1 of these processes may, perhaps, be duplicated or replaced by several thinner appendages. Membrane of the shell smooth or indistinctly granular.

Dimensions.—Diameter of shell *c.* 35-45 μ, length of processes 20-30 μ, breadth of large processes 8-13 μ, length of narrow processes 18-25 μ.

H. rigaudae differs considerably from *H. cinctum* Klumpp, the type species of the genus: (i) in the general form of the large processes, which are rarely cylindrical but usually slightly narrowed and then widened at their extremities, which are always closed; (ii) in the smaller number of narrow although apparently more robust equatorial processes. Klumpp (1953) has indicated that the large cornet-shaped appendages are either widely open or prolonged into a point with a small terminal opening, the latter apparently the normal condition, the former more likely the result of imperfect preservation.

H. rigaudae has been directly compared with examples of *H. cinctum* from an Oligocene clay of Innien (Germany) thanks to the kindness of Mr. A. Elger of Eutin (Germany), whose excellent preparations in the Laboratoire de Micropaléontologie, Paris, contain a number of good examples of this species. These Oligocene plesiotypes of *H. cinctum* are identical with those described from the Upper Eocene by Klumpp. In certain examples the distal opening of the large conical process is well shown although it is not possible to demonstrate conclusively that the opening is constant and natural.

The second species of *Hystrichokolpoma* mentioned by Klumpp has been observed in a pebble from the Senonian flint of the Paris basin

(Deflandre, unpublished data). It is quite distinct from *H. rigaudae* and is nearer to *H. cinctum*, from which it can be distinguished by the structure of the equatorial zone.

H. rigaudae is relatively common in the Birregurra deposit at 514-516 ft.

Genus MICRHYSTRIDIUM Deflandre

This genus is certainly well represented in Australian Tertiary sediments but in the present work it has been deliberately neglected, partly because the method of mounting has sometimes precluded the use of an oil immersion objective, indispensable in a study of *Micrhystridium*, and partly because the amount of work a study of all the forms present would entail is out of all proportion to the results immediately utilizable.

However, several forms have already been cited by one of us (I.C.C.) and several others have incidentally been noted.

MICRHYSTRIDIUM cf. AMBIGUUM Deflandre

Plate 8, Fig. 2

Micrhystridium ambiguum Deflandre, 1937, Ann. Paléont. 26: 33, pl. 16, figs. 8 and 9.

Micrhystridium cf. *ambiguum* Defl. in Cookson, 1953, pl. 2, fig. 33, Nat. Mus. Vic. P15635.

Micrhystridium sp. sec. Cookson, 1953, pl. 2, fig. 34.

Lower Eocene: Princetown Member of Dilwyn Clay, Vic.

? Middle Eocene: Anglesea, Vic.

Comparison of the Australian form, shown in Plate 8, Figure 2, with the type of *M. ambiguum* Defl. shows that it differs in the length of the processes (about 7 μ instead of 3-3.5 μ). Also the density of the processes is not so great and the extremities do not form such a clear concentric circle as in *M. ambiguum*. However, the two forms are very close and a better knowledge of the Senonian type will perhaps permit an identification of this species.

It is possible that the second specimen mentioned above under the name *Micrhystridium* sp. may also belong to the same group; some of the processes of the photographed specimen are imperfect but others have clearly forked apices.

Types.—Holotype: Coll. G. Deflandre, Paris, AF70.

MICRHYSTRIDIUM cf. INCONSPICUUM Deflandre

Hystrichosphaera inconspicua Deflandre, 1935, Bull. Biol. 69: 233, pl. 9, figs. 11 and 12.

Micrhystridium inconspicuum Deflandre, 1937, Ann. Paléont. 26: 32, pl. 12, figs. 11-13.

Paleocene to Lower Eocene: Pebble Point Formation, Vic.

? Lower Eocene: Birregurra, Vic., bore No. 1.

Different forms of *Micrhystridium* belonging to the group of *M. inconspicuum* Defl. sensu lato have been observed in the abovementioned deposits. Their occurrence demonstrates that this minute type was represented in the Tertiary. *M. inconspicuum* and species very like it are abundant in the French Jurassic flints (Valensi 1953), and analogous forms existed in the Silurian (*M. parinconspicuum* Defl.) and Carboniferous (*M. bacilliferum* Defl.).

Types.—Holotype: Coll. G. Deflandre, Paris, AJ1.

MICRHYSTRIDIUM PACHYDERMUM sp. nov.

Fig. 37

Lower Cretaceous: Onepah Station, N.S.W.

Paleocene to Lower Eocene: Pebble Point Formation, Vic.

Shell globular or ellipsoidal; wall thick, regularly covered with short, conical, pointed spines.

Dimensions.—18-19 μ by 16-17 μ.

The occurrence of a thick wall is unusual in the genus *Micrhystridium*, and it is thought that the specimens included in this new species may be spores. They have been described here because of their relative frequency in the Onepah deposit.

MICRHYSTRIDIUM cf. RETICULATUM Deflandre

Plate 5, Figs. 11 and 12

Micrhystridium reticulatum Deflandre, 1937, Ann. Paléont. 26: 34, pl. 17, figs. 5 and 6.

Micrhystridium cf. *reticulatum* Defl. sec. Cookson, 1953, pl. 2, figs. 31-32.

Lower Eocene: Princetown Member of Dilwyn Clay, Vic.

No other specimen similar to this type has been found during the present research. The holotype of *M. reticulatum* possesses pointed processes, so that the Australian form, in which the processes are clearly truncate, cannot be identified with it. However, the shape of the meshes is very similar, and it is almost certainly a closely related form.

Types.—Holotype: Coll. G. Deflandre, Paris, AH23.

MICRHYSTRIDIUM cf. STELLATUM Deflandre

Figs. 38 and 39

Micrhystridium stellatum Deflandre, 1942, C. R. Acad. Sci., Paris 215: 476, figs. 7 and 8.

Paleocene to Lower Eocene: Pebble Point Formation, Vic.

It seems unlikely that all the forms classified under the name of *M.* cf. *stellatum* are really the true *M. stellatum* Defl. of the Silurian. However, it is very difficult and often impossible to find characters sufficiently distinctive to separate the forms occurring in the younger sediments into distinct species. Valensi (1953, Plate 9, Figs. 30-32) has already referred

French Jurassic specimens to *M.* cf. *stellatum.* The Australian forms strongly resemble the latter, but many of the horns have capitate rather than pointed apices. However, the differences between the methods of preparation in the two instances may possibly account for these slight differences, and, at least provisionally, the Australian specimens will be placed near the Silurian species.

Dimensions.—Shell 14-19 μ, processes 11-14 μ.

Types.—Holotype: Coll. G. Deflandre, Paris, AY14.

Genus CANNOSPHAEROPSIS O. Wetzel emend. Deflandre

CANNOSPHAEROPSIS AEMULA Deflandre

Plate 3, Fig. 1

Hystrichosphaeridium aemulum Deflandre, 1938, C. R. Acad. Sci., Paris **204**: 688, fig. 6.

Cannosphaeropsis aemula Deflandre, 1947, C. R. Acad. Sci., Paris **224**: 1576.

Lower Cretaceous: Era River district, Papua, New Guinea. W.451 (see Section VI (*a*)).

The best of the New Guinea specimens does not differ appreciably from the French Jurassic forms of *C. aemula,* which themselves have a variable appearance. It resembles both the holotype (Deflandre 1938, Plate 10, Figs. 5 and 6) and paratype (loc. cit., Plate 9, Fig. 12) from the Oxfordian.

Types.—Holotype: Coll. G. Deflandre, Paris, AM44.

CANNOSPHAEROPSIS FENESTRATA sp. nov.

Fig. 43; Plate 3, Fig. 2

Upper Cretaceous (Senonian): Gingin, W.A.

Shell apparently ellipsoidal; membrane thin, smooth, with a number of solid processes that are distally united with one another; localized portions of the transverse trabeculae are thin; strongly flattened and perforated by rounded openings of variable size.

Dimensions.—Holotype: shell 64 by 46 μ, estimated overall diameter about 128 μ.

C. fenestrata is so different from the other species of *Cannosphaeropsis* that it cannot be compared with any of them.

CANNOSPHAEROPSIS CAULLERYI Deflandre

Plate 7, Fig. 8

Hystrichosphaeridium caulleryi Deflandre, 1938, Trav. Stat. Zool. Wimereux **13**: 189, pl. 11, figs. 2 and 3.

Cannosphaeropsis caulleryi Deflandre, 1947, C. R. Acad. Sci., Paris **224**: 1576.

Cannosphaeropsis cf. *caulleryi* Defl. sec. Cookson, 1953, pl. 2, figs. 35-40, p. 117.

Paleocene to Lower Eocene: Pebble Point Formation, Vic.

Lower Eocene: Birregurra, Vic., bore No. 1 at 842-843 ft; Dilwyn Clay, Vic.; Princetown Member of Dilwyn Clay, Vic.

? Middle Eocene: Anglesea, Vic.

The specimens mentioned previously by one of us (I.C.C.) have been re-examined and compared with Jurassic types of *C. caulleryi.* There is practically no difference between the ensemble of Australian forms and these types. *C. caulleryi* seems to be relatively common. In view of this distribution it is curious to note its absence, or at least extreme rarity, in the European Cretaceous, where, in spite of the large number of flints already studied, *C. caulleryi* has not as yet been met with.

Types.—Holotype: Coll. G. Deflandre, Paris, AM22.

CANNOSPHAEROPSIS URNAFORMIS Cookson

Plate 7, Figs. 9 and 10

Cannosphaeropsis urnaformis Cookson, 1953, Mem. Nat. Mus., Melb. 18: 118, pl. 2, figs. 41-43.

? Lower Eocene: Birregurra, Vic., bore No. 1 at 833-834 and 876-877 ft.

? Middle Eocene: Anglesea, Vic.

This species has been described as follows (Cookson 1953): "The type specimen is a smooth, ovoid shell 44 by 55 μ with approximately twelve short, broad, radially arranged vase-shaped appendages. The latter measure about 20 μ across the base and about 30 μ across the rim, and are 15-18 μ long. The walls of the appendages are much perforated, the holes frequently extending from the rim to the prominent angular thickening present at the point of junction of an appendage with the shell membrane. The rim is entire and slightly fluted. The appendages of this specimen are free from one another. A second example, however, suggests that they may not have always been so, since two of its appendages are definitely attached to one another by a short and delicate strand. The surface of the shell is finely granular."

It is equally possible to interpret each "vase-shaped appendage" as a series of processes of which the bases are coalescent (as in *Hystrichosphaeridium placacanthum*) and the distal extremities reunited by trabeculae as in *Cannosphaeropsis aemula* Defl. In *C. aemula,* however, the processes or groups of processes are all connected together by filaments, whereas in *C. urnaformis* the basket-like appendages usually appear to be free from one another. However, the example cited by Cookson (1953, Plate 2, Fig. 43) in which two of the appendages are united by a short connecting strand, which has been critically re-examined, demonstrates the probability that this was not always the case. Under this circumstance the attribution to the genus *Cannosphaeropsis* O. Wetzel emend. Deflandre seems to be well justified.

Types.—Holotype: National Museum, Melbourne, P15637.

Genus CYCLONEPHELIUM gen. nov.

Shell spheroidal, flattened, with an equatorial ornamentation that extends for varying distances from the equator but never to the poles. The ornament is composed of processes that are either distinct or close and confluent and sometimes connected by more or less broad trabeculae. Shell often provided with a large ill-defined lateral opening.

Genotype, *Cyclonephelium compactum* sp. nov.

A second Australian species, *Cyclonephelium distinctum* sp. nov., and two species which Pastiels (1948) has placed in the genus *Membranilarnax* O. Wetzel, also fall into the new genus *Cyclonephelium*. Pastiels' species are: *Cyclonephelium exuberans* sp. nov. syn. *Membranilarnax pterospermoides* A. Pastiels 1948 non O. Wetzel 1933; and *Cyclonephelium pastielsi* sp. nov. syn. *Membranilarnax* cf. *liradiscoides* Pastiels 1948 non O. Wetzel.

Deflandre has examined Wetzel's types of *Membranilarnax* and, as O. Wetzel has written, has clearly recognized in them the existence of a second, generally thin membrane which entirely surrounds the primary shell, to which it is attached by clearly defined processes. This character does not exist in the two forms described by Pastiels.

Furthermore, the type of the species *Membranilarnax pterospermoides* O. Wetzel (type species of the genus) has not at all the appearance of a *Cyclonephelium*, in spite of the indications given in the diagnosis that the majority of the processes are in the equatorial plane. *Cyclonephelium* is readily distinguished from *M. pterospermoides* by the flatness of its shell, the unornamented polar regions, and the localization of the ornamentation to the equator. The type of ornamentation itself approaches that of certain species of *Hystrichosphaeridium* and *Cannosphaeropsis*.

CYCLONEPHELIUM COMPACTUM sp. nov.

Figs. 44-46; Plate 2, Figs. 11-13

Lower Cretaceous: Onepah Station, N.S.W.

Upper Cretaceous (Senonian): Gingin, W.A.

The appendages forming the equatorial ornamentation are generally short and joined to one another, forming lamella-like projections arranged either parallel to the equator of the shell or in the form of an irregular network. Sometimes a series of processes are joined by short trabeculae.

The surface of the shell is slightly punctate.

Dimensions.—Shell 61-72 μ, height of ornament 5-10 μ, overall diameter 72-87 μ.

CYCLONEPHELIUM DISTINCTUM sp. nov.

Figs. 47 and 48; Plate 2, Fig. 14

Upper Cretaceous (Senonian): Gingin, W.A.

Ornamentation typically consisting of numerous short, solid appendages of variable width, the apices of which are either bluntly pointed, capitate, enlarged, or forked; rarely the processes are joined to one another forming short lamellae. They are irregularly disposed, most numerous at the equator and becoming progressively fewer towards the poles, from which they are entirely absent.

Surface of shell distinctly punctate.

Dimensions.—Diameter of shell 64-97 μ, length of appendages 2.5-18 μ.

It is sometimes difficult to separate *C. compactum* from *C. distinctum,* surely two closely related species, but when a series of individuals is observed the distinction between them becomes clear. In a few examples of *C. distinctum* lamella-like appendages have been observed amongst the typical processes of this species, but so far isolated appendages similar to those of *C. distinctum* have not been seen in *C. compactum.*

Family **PTEROSPERMOPSIDAE**

Genus PTEROSPERMOPSIS W. Wetzel

The following diagnosis given by W. Wetzel (1952) is both precise and comprehensive: capsule of organic matter, globular and provided with an equatorial flange. The name of the genus indicates a resemblance to the genus *Pterosperma* Pouchet, a component of living plankton of which the systematic position still remains enigmatical. The two species of Pouchet, *Pterosperma rotundum* and *P. ovatum,* are not related to the genotype *Pterospermopsis danica* W. Wetzel, the latter corresponding more closely to *Pterosperma moebiusi* Joergensen than to any of the other living forms described.

Pterospermopsis danica was found in the Danian flints of north Germany both by W. Wetzel and by O. Wetzel (1933, Plate 3, Fig. 22).

It is also mentioned by Klumpp (1953, Plate 19, Fig. 7) as definitely occurring in a north German Eocene clay. More recently Eisenack (1954) has described a second species of Oligocene age.

Both these species are very different from those now to be described, which are noticeably smaller. One, *Pterospermopsis ginginensis,* is only known from a single example, but the others are not rare and may eventually have a stratigraphical value.

PTEROSPERMOPSIS AUSTRALIENSIS sp. nov.

Figs. 52 and 53; Plate 3, Fig. 4

Lower Cretaceous: Onepah Station, N.S.W.

.Cell circular in apical view, ellipsoidal in lateral view, provided with a relatively large undulating and radially folded equatorial wing; contour of wing circular. Surface of shell smooth.

Dimensions.—Diameter of shell 10-18 μ, overall diameter 25-33 μ, ratio of shell to wing 2.4-3.3.

PTEROSPERMOPSIS GINGINENSIS sp. nov.

Fig. 49

Upper Cretaceous (Senonian): Gingin, W.A.

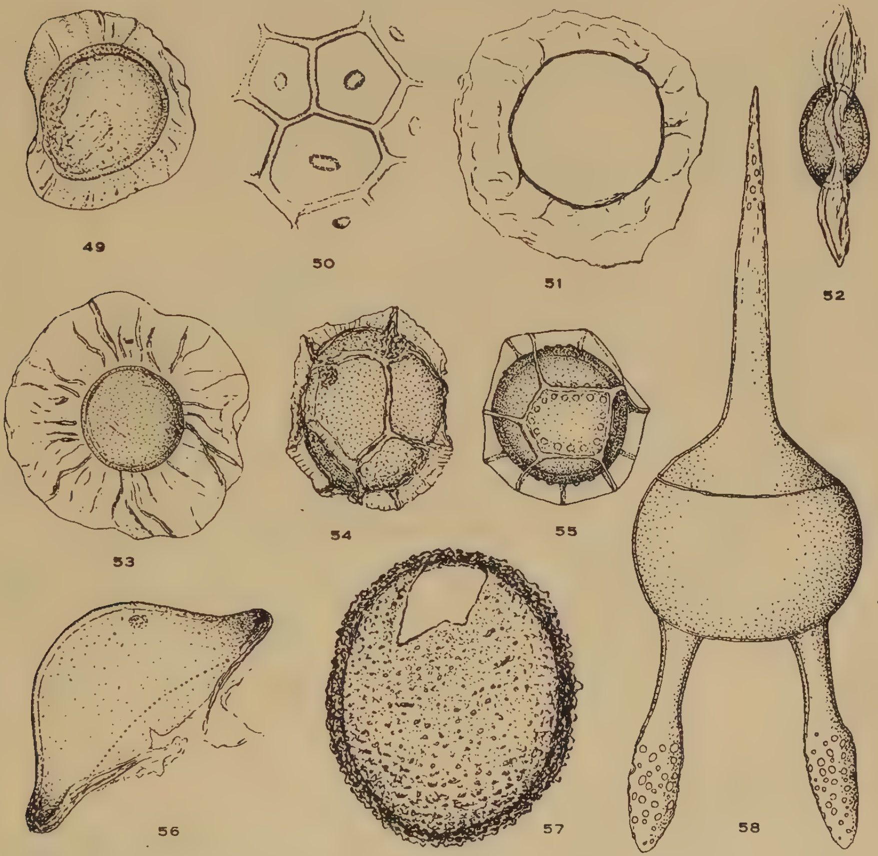

Fig. 49.—*Pterospermopsis ginginensis* sp. nov. Gingin, W.A. × 622. Fig. 50.—*Cymatiosphaera punctifera* sp. nov. Part of the membrane of the type figured in Plate 7, Fig. 14. Birregurra, Vic. × 1545. Fig. 51.—*Membranilarnax clathroderma* sp. nov. Optical section of the type figured in Plate 7, Fig. 6. Birregurra, Vic. × 622. Figs. 52-53.—*Pterospermopsis australiensis* sp. nov. × 982. Fig. 52.—Lateral view. Onepah Station, N.S.W. Fig. 54.—*Cymatiosphaera* cf. *wetzeli* Defl. Birregurra, Vic. × 622. P16408. Fig. 55.—*Cymatiosphaera imitata* sp. nov. Gingin, W.A. Holotype. × 622. P16228. Fig. 56.—*Epicephalopyxis indentata* sp. nov. Lateral view. Princetown Member of Dilwyn Clay, Vic. × 622. Fig. 57.—*Leiosphaera scrobiculata* sp. nov. Gingin, W.A. × 622. Fig. 58.—*Odontochitina cribropoda* sp. nov. Reconstruction after the specimen figured in Plate 3, Fig. 8. Nelson Bore, Vic. × 622.

Shell oval in apical view, probably elliptical in lateral view, provided with a relatively narrow, somewhat irregularly folded wing; contour of wing elliptical (deformed in the single specimen observed). Surface of shell slightly punctate.

Dimensions.—Diameter of shell 26 μ, overall diameter 41 μ, ratio of shell to wing 1.6.

PTEROSPERMOPSIS MICROPTERA sp. nov.

Plate 6, Fig. 8

Paleocene to Lower Eocene: Pebble Point Formation, Vic.

? Middle Eocene: Anglesea, Vic.

Eocene: Castle Cove, Vic.

Lower Tertiary: near Denmark, W.A.

Middle Miocene (Balcombian): Gellibrand Clay near Princetown, Vic.

Shell circular in apical view, broadly ellipsoidal in lateral view. Equatorial wing narrow, more or less undulating, and radially folded, contour of wing circular or slightly undulate. Surface of shell smooth.

Dimensions.—Diameter of shell 13-15.5 μ, overall diameter 21-28 μ, ratio of shell to wing 1.6-1.86.

Genus CYMATIOSPHAERA O. Wetzel emend. Deflandre

Since this genus has only recently been reviewed and enlarged (Deflandre 1954) it may be useful to repeat the new diagnosis.

Shell globular, spherical or ellipsoidal, the external surface divided into polygonal fields by membranes perpendicular to the surface, without any equatorial differentiation of the fields or processes of any kind; the outer margins of the membranes straight or slightly concave, entire, serrated or somewhat corroded. Surface of shell smooth, punctate, or granular.

Dimensions.—Very variable, from a few microns to more than 100 μ, ridges included.

The genotype, *Cymatiosphaera radiata* O. Wetzel, came from a Cretaceous flint of northern Germany. The other specimens, certain of which were previously classed in the genus *Micrhystridium* Deflandre, are distributed from the Silurian to the Cretaceous. Now for the first time these forms can be recorded from the Tertiary.

CYMATIOSPHAERA IMITATA sp. nov.

Fig. 55

Upper Cretaceous (Senonian): Gingin, W.A.

Shell globular with a thick wall and 12-14 pentagonal fields; membranes high, transparent, and smooth, bearing on either sides of their bases a line of small rounded knobs.

Dimensions.—Diameter of shell 29-30 μ; overall diameter 38-41 μ.

This species is morphologically related to the living planktonic microorganism *Pterosphaera dictyon* Joergensen, but the latter has pores all over the ridges and in the centre of the fields instead of two lines of small prominences. *P. dictyon* has a diameter of 56-64 μ.

CYMATIOSPHAERA PUNCTIFERA sp. nov.

Fig. 50; Plate 7, Fig. 14

? Lower Eocene: Birregurra, Vic., bore No. 1 at 837-838 ft.

Shell globular with a relatively thick wall and 17 to 18 5- or 6-sided fields; membranes low, transparent, smooth, each field with a prominent, irregular central thickening.

Dimensions.—Diameter of shell *c.* 18 μ, overall diameter 23 μ.

CYMATIOSPHAERA cf. WETZELI Deflandre

Fig. 54

Ornamented shell secundum O. Wetzel, 1933, Palaeontographica A 78: pl. 4, fig. 7.
Cymatiosphaera wetzeli Deflandre, 1954, C. R. Soc. Géol. Fr. No. 12: 258.

Miocene or older: Birregurra, Vic., bore No. 1 at 514-516 ft.

Lower Eocene: Princetown Member of Dilwyn Clay, Vic.

The specimen figured here, of which both the shell and raised membrane are finely punctate, is very close to the specimen illustrated by O. Wetzel (1933) in Plate 4, Figure 7. The number of fields is not high. The overall diameter (max. 44 μ) is lower than that given by O. Wetzel (52 μ for the form taken as the type, and 80-100 μ for the other specimens), all specimens being found in Cretaceous flints of northern Germany.

A second example from the Princetown Member of the Dilwyn Clay measures 38 by 33 μ.

Types.—Holotype: Coll. O. Wetzel, Eutin, No. 242.

CYMATIOSPHAERA EUPEPLOS (Valensi) Deflandre

Plate 6, Fig. 9

Micrhystridium eupeplos Valensi, 1948, Bull. Soc. Géol. Fr. 18: 542, fig. 3 (1-6).
Cymatiosphaera eupeplos (Valensi) Deflandre, 1954, C. R. Soc. Géol. Fr. No. 12: 258.

Lower Cretaceous: Onepah Station, N.S.W.

Upper Cretaceous (Senonian): Gingin, W.A.

Paleocene to Lower Eocene: Pebble Point Formation, Vic.

Miocene or older: Birregurra, Vic., bore No. 1 at 514-516 ft.

Middle Miocene: Balcombe Bay, Vic.

The variations admitted by Valensi (1953) amongst the group of Jurassic specimens included in *C. eupeplos* permit us to place in this species a series of very similar forms of variable size that have been met with in Australian Cretaceous and Tertiary deposits. In the examples from Onepah Station (Lower Cretaceous) and the Pebble Point Formation (Paleocene to Lower Eocene) the wall of the shell is clearly thicker than in the forms figured by Valensi.

The smallest specimen (Miocene of Balcombe Bay, Plate 6, Fig. 9) measures only 10 μ overall; the largest, 17 μ (Birregurra bore), has a thin wall and is identical with a specimen in a Senonian flint of the Paris basin (Deflandre, unpublished data).

Types.—Holotype: Coll. G. Deflandre, Paris, BS22.

Genus MEMBRANILARNAX O. Wetzel

MEMBRANILARNAX ANGUSTIVELUM sp. nov.

Plate 7, Figs. 4 and 5

? Lower Eocene: Birregurra, Vic., bore No. 1 at 791-795 and 837-838 ft.

Shell ellipsoidal or almost globular, with a rather thick membrane enveloped in a 2nd delicate membrane that is supported by short processes. These processes are either simple or more often grouped so as to form twisted lamellae which have a worm-like appearance in surface view. External outline irregularly wavy.

Dimensions.—Holotype (Plate 7, Fig. 4): shell 54 by 41 μ, overall 67 by 54 μ, height of processes *c.* 5 μ. Range: shell alone 41-59 μ, overall diameter 51-72 μ.

This species corresponds perfectly to the general meaning of the genus *Membranilarnax*, and differs very clearly from the known species, particularly in the short distance that separates the outer veil from the true shell membrane.

MEMBRANILARNAX CLATHRODERMUM sp. nov.

Fig. 51; Plate 7, Fig. 6

? Lower Eocene: Birregurra, Vic., bore No. 1 at 842-843 ft.

Shell practically spherical with an angular outline and thin wall surrounded by a 2nd very fine membrane that is indistinctly punctate and perforated with relatively large rounded holes. External membrane attached to the shell, not by individual processes but by membranous lamellae, which form a kind of wide-meshed reticulate surface design wholly independent of the abovementioned holes. External outline irregularly rounded, not exactly concentric with the shell.

Dimensions.—Diameter of shell 34 μ, overall diameter 46 μ.

At first sight this species seems to closely resemble *Membranilarnax* cf. *liradiscoides* (sec. Deflandre, 1937, Plate 16, Fig. 10) from a Senonian flint of the Paris basin, the species having much the same dimensions, but direct comparison of the two specimens shows important differences. The external membrane of the Senonian specimen is not clathrate, the trabeculae which attach it to the shell are thicker and more closely arranged, and above all, their insertion on the shell is more strongly marked. However, the two forms are clearly closely related.

Genus PTEROCYSTIDIOPSIS Deflandre

PTEROCYSTIDIOPSIS VELATA sp. nov.

Plate 8, Fig. 8

Probably Lower Tertiary: near Denmark, W.A.

Central shell ellipsoidal with a slightly thickened membrane, from which groups of radially arranged fibrils diverge towards the periphery of the relatively wide, delicate, finely reticulate membrane that envelops the shell.

Dimensions.—Central shell *c.* 79 by 64 μ; overall length 125 μ.

The type of this new species is very imperfect but, nevertheless, its characters are sufficiently defined to indicate a relationship with *Pterocystidiopsis ornata* Defl. known from the Cretaceous flints of Paris. The generic attributes of *Pterocystidiopsis* have been discussed (Deflandre 1937, p. 92). The provisional placing of both species in this genus is justified by the insufficient number of individuals studied.

Family **LEIOSPHAERIDAE**

Genus LEIOSPHAERA Eisenack

LEIOSPHAERA SCROBICULATA sp. nov.

Fig. 57; Plate 3, Fig. 3

Upper Cretaceous (Senonian): Gingin, W.A.

Paleocene to Lower Eocene: Pebble Point Formation, Vic.

Lower Eocene: Princetown Member of the Dilwyn Clay, Vic.

Shell ovoidal or ellipsoidal, generally with an irregular polygonal opening at the narrower end, the cover of which is sometimes in position. Wall of shell about 3-5 μ thick, finely punctate, and closely dotted with irregular scrobiculi.

Dimensions.—Cretaceous examples: 61-94 μ long, 48-72 μ broad. Tertiary examples: 38-54 μ long, 31-41 μ broad.

This characteristic microfossil is easily recognized by its ovoidal form from other species of *Leiosphaera*, which, according to Eisenack (1938*b*), are all completely spherical. But as this genus is obviously a heterogenous assemblage of unrelated types, and of purely morphological significance, it seems useful to enlarge its conception by including in it any elliptical or ovoidal forms (without true appendages) the length of which is less than double the breadth.

More elongated types should be placed in the genus *Leiofusa* Eisenack.

INCERTAE SEDIS

Genus ODONTOCHITINA Deflandre

ODONTOCHITINA OPERCULATA (O. Wetzel) Deflandre

Plate 3, Figs. 5 and 6

Ceratium operculatum O. Wetzel, 1933, Palaeontographica A 177: 170, pl. 2, fig. 21.
Odontochitina silicorum Deflandre, 1935, Bull. Biol. 69: 234, pl. 9, figs. 8-10; Deflandre, 1937, Ann. Paléont. 26: pl. 18, figs. 8-13.
Odontochitina operculata (O. Wetzel) Deflandre.

Lower Cretaceous: Onepah Station, N.S.W.

Lower Cretaceous: Era River, Papua, New Guinea. W.451 (see Section VI(*a*)).

The Australian specimens are often folded and deformed, demonstrating the relative sensitivity of these organisms to the treatment to which they have been subjected. However, a few complete specimens have been found in which a globular portion with 2 horn-like appendages and an operculum with a single longer appendage are clearly recognizable.

Dimensions.—Body *c.* 48 by 44 μ, appendages 72-116 μ long.

Types.—Holotype: Coll. O. Wetzel, Eutin, No. 339 (type of *C. operculatum*). Plesiotype: Coll. G. Deflandre, Paris, AH98 (type of the genus *Odontochitina*).

ODONTOCHITINA CRIBROPODA sp. nov.

Fig. 58; Plate 3, Figs. 7-11

Upper Cretaceous: Gingin, W.A.

? Upper Cretaceous: Nelson Bore, Vic., at 5782 ft.

The globular body is provided with 2 divergent club-like appendages, the distal portions of which are perforated by a large number of rather regularly arranged small openings of irregular size and shape, while the proximal portions are entire, thicker-walled, and slightly constricted. The operculum or superior portion of the organism bears a long thorn-like appendage also perforated at its extremity.

Dimensions.—Width of body about 74-87 μ, appendages from 53 to 110 μ long, perforated distal region 20-76 μ long and 10-26 μ broad.

Genus EPICEPHALOPYXIS Deflandre

The two microorganisms referred to this genus are morphologically conformable with it, but it is doubtful whether they are related either to one another or to *E. adhaerens* Defl., from the French Upper Cretaceous, the only other species. However, in spite of our complete ignorance of the biological significance of these forms, their relative frequency demands that they be considered and described.

EPICEPHALOPYXIS INDENTATA sp. nov.

Fig. 56; Plate 9, Figs. 5-7

? Paleocene to Lower Eocene: Nelson Bore, Vic., at 3874 ft.

Paleocene to Lower Eocene: Pebble Point Formation, Vic.

Lower Eocene: upper part of Dilwyn Clay, Vic.

Lower Eocene: Princetown Member of Dilwyn Clay, Vic.

? Lower Eocene: Birregurra, Vic., bore No. 1.

? Lower Eocene: Nelson Bore, Vic., at 992 ft.

? Middle Eocene: Anglesea, Vic.

Upper Eocene or older: Castle Cove, Vic.

Miocene or older: Birregurra, Vic., bore No. 1 at 514-516 ft.

Lower Tertiary: near Denmark, W.A.

Organism more or less deeply cap- or dome-shaped, with a circular or elliptical outline provided with a relatively narrow, smooth, irregularly notched, slightly wavy rim. Surface membrane finely granular.

Dimensions.—51-74 by 43-69 μ, extremes 51 by 51 μ, 74 by 59 μ.

EPICEPHALOPYXIS SPECTABILIS sp. nov.

Plate 3, Figs. 12-14

Lower Cretaceous: Era River district, Papua, New Guinea. W.451 (see Section VI(*a*)).

Body of organism considerably compressed, irregularly elliptical in outline, membrane thin, 2-layered, outer one smooth, ornamented with a relatively wide lace-like edge. Marginal band formed by the union of processes connected with one another by their distal extremities in such a way as to form a more or less distinct peripheral network.

Dimensions.—Type: overall measurements 110 by 84 μ, lace-like margin *c.* 8 μ.

? CERATIUM cf. FUSUS forma INCERTA Deflandre

Plate 8, Fig. 1

Ceratium cf. *fusus* (Ehr.) forma *incerta* Deflandre, 1936, Ann. Paléont. 25: 40, pl. 10, figs. 8 and 9.

Paleocene to Lower Eocene: Pebble Point Formation, Vic.

Deflandre (1936) gave the name forma *incerta* to a microorganism in Cretaceous flints similar to those already observed by O. Wetzel (1933), who distinguished several types (*f. rhomboides*, *f. ovatum*, *f. nodosum*, *f. filosum*).

It is very improbable that this organism and the one present in Australia actually belong to the group of *Ceratium fusus* Clap & Lachm. Even its reference to the genus *Ceratium* is also extremely doubtful. Possibly it would be preferable, pending a precise statement of its affinity, to classify it as Incertae Sedis. The appearance of the figured Australian example is reminiscent of the genus *Odontochitina*.

VI. Analytical List of Samples

(*a*) *Lower Cretaceous*

(i) *Near Era River, Papua, New Guinea.*—Indurated carbonaceous sandstones. No details are available other than that the Australasian Petroleum Company's two samples L.P.E.821 and W.451 came from beneath Miocene and Eocene limestones. Neither sample is rich in microfossils, the former being distinctly the poorer. A few badly preserved pteridophyte spores and coniferous pollen grains are present, but no dicotyledonous types have been observed.

The microplankton includes:

L.P.E.821. *Hystrichosphaeridium salpingophorum* (one example),
W.451. *Cannosphaeropsis aemula,*
Epicephalopyxis spectabilis,
Odontochitina cf. *operculata* (a fragment).

(ii) *Onepah Station, N.S.W.*—The exact age of the sample dug from a well sunk on Onepah Station in north-western New South Wales is not definitely proved, but Mr. H. O. Fletcher, Curator of Fossils, the Australian Museum, Sydney, has very kindly provided the following information about it: "A few miles to the south of the locality definite Lower Cretaceous marine fossils occur on the surface with strata dipping to the north, so that the Onepah well sediments are above them. However, in the well material there are small ammonites and other small bivalves and gastropods not definitely identified but certainly of a Lower Cretaceous appearance . . . The Onepah well sediments would be no great distance above the definite Lower Cretaceous beds."

The spore and pollen content of the deposit is high and quite distinct from all known Tertiary microfloras. Pteridophyte spores are numerous and included amongst them are examples of the schizaeaceous spore *Mohriosporites australiensis* Cookson, also recovered from Lower Cretaceous coals of the Burrum and Styx River districts of Queensland, and from pre-Tertiary deposits in South Australia and Victoria (Cookson 1953, 1954*a*).

Most of the podocarpaceous pollen types are distinct from those occurring in Australian Tertiary sediments. No angiosperm pollen grains have been recognized.

The microplankton includes:

DINOFLAGELLATA: *Gonyaulax* cf. *wetzeli; G.* sp. ind.; *Hystrichodinium oligacanthum*; *Dinopterygium cladoides.*

HYSTRICHOSPHAERIDAE: *Hystrichosphaera furcata*; *Hystrichosphaera speciosa*; *Hystrichosphaera wetzeli*; *Hystrichosphaeridium recurvatum*; *Hystrichosphaeridium complex*; *Hystrichosphaeridium pulcherrimum*; *Hystrichosphaeridium isocalamus*; *Hystrichosphaeridium fimbriatum*; *Micrhystridium pachydermum*; *Micrhystridium* cf. *inconspicuum*; *Cyclonephelium compactum.*

PTEROSPERMOPSIDAE: *Pterospermopsis australiensis; Cymatiosphaera eupeplos.*

INCERTAE SEDIS: *Odontochitina operculata.*

(*b*) *Upper Cretaceous* (*Senonian*)

(i) *Gingin, W.A.*—Lower Greensand. According to Teichert (1946) this deposit "is very rich in glauconite and has furnished very few fossils. Its transition to the overlying chalk is somewhat gradual, the chalk in places being extremely fossiliferous". During the present investigation coccoliths have been observed in preparations of the chalk. The pollen and spore content of the Greensand is too low and uncertain in origin for present comment.

The microplankton includes:

DINOFLAGELLATA: *Gymnodinium* cf. *heterocostatum*; cf. *Palaeoglenodinium* sp.; *Palaeohystrichophora multispina; Palaeohystrichophora minuta.*

HYSTRICHOSPHAERIDAE: *Hystrichosphaera ramosa*; *Hystrichosphaeridium recurvatum; Hystrichosphaeridium complex; Hystrichosphaeridium polytrichum*; *Hystrichosphaeridium flosculus*; *Hystrichosphaeridium heteracanthum*; *Cannosphaeropsis fenestrata*; *Cyclonephelium compactum*; *Cyclonephelium distinctum.*

PTEROSPERMOPSIDAE: *Pterospermopsis ginginensis*; *Cymatiosphaera imitata.*

LEIOSPHAERIDAE: *Leiosphaera scrobiculata.*

INCERTAE SEDIS: *Odontochitina cribropoda.*

(*c*) ? *Upper Cretaceous to Eocene*

(i) *Nelson Bore, Vic.*—The carbonaceous sandstones from the Nelson Bore, examined during the present investigation, are those situated between 992 and 6192 ft. Recently this portion of the bore has been included above the equivalents of the Pebble Point Formation in southern Victoria by the Geological Surveys of South Australia and Victoria (Boutakoff and Sprigg 1953). However, there are reasons for thinking that this assignment is not absolutely correct and that the lower sections of the bore, that is, from 3723 to 6192 ft, may be Lower Eocene or Paleocene to Upper Cretaceous in age (see Section IV).

The pollen and spore content at 992 ft is well characterized and very similar to microflora C of the Birregurra bore deposits between 760 and 900 ft, the Anglesea sandstone, and the Princetown Member of the Dilwyn Clay.

Pollen grains and spores are very sparse in the deeper sections of the bore and their stratigraphical value is difficult to assess. However, as far as can be judged at present, angiosperm pollen types decrease in number with increasing depth, a feature observed during the study of the Birregurra bore (Cookson 1954*a*). The sporomorph *Triorites edwardsii*, which occurs in the Pebble Point Formation (Paleocene to Lower Eocene), has been observed at 3723, 3874, and 4025 ft. Traces of the presence of *Mohriosporites australiensis* Cookson at 5782 and 6065 ft supports but does not prove an Upper Cretaceous age; more positive evidence is afforded by the contained microplankton, which is as follows:

6192 ft

HYSTRICHOSPHAERIDAE: *Hystrichosphaeridium complex*; *Hystrichosphaeridium heteracanthum.*

5782 ft

HYSTRICHOSPHAERIDAE: *Hystrichosphaeridium complex*; *Hystrichosphaeridium heteracanthum.*

INCERTAE SEDIS: *Odontochitina cribropoda.*

3874 ft

DINOFLAGELLATA: *Deflandrea bakeri* f. *pellucida.*

HYSTRICHOSPHAERIDAE: *Hystrichosphaeridium heteracanthum.*

992 ft

HYSTRICHOSPHAERIDAE: *Hystrichosphaera ramosa; Hystrichosphaera cingulata.*

INCERTAE SEDIS: *Epicephalopyxis indentata.*

(*d*) *Paleocene to Lower Eocene*

(i) *Moonlight Head-Princetown District, Vic.*—Wangerrip Group. The geological ages cited for the Older Tertiary sediments referred to below are based largely on recent conclusions (Baker 1953) concerning the age relationships of the Wangerrip Group in the Moonlight Head-Princetown district of south-western Victoria.* Taking into account: (*a*) Baker's conclusions (1953); (*b*) Singleton's earlier reference (1943, p. 267) of certain pelecypods from this area to the "Lower Eocene or possibly Paleocene"; (*c*) Teichert's (1943, p. 258) reference of certain of the nautiloids from the same area to the "late Cretaceous"; and (*d*) Parr's observations (see Baker 1944, p. 87) that there are similar foraminiferal assemblages in the Pebble Point Formation and in the Rivernook Member some 500 ft stratigraphically higher in the Wangerrip Group—the following ages are employed for the microplankton discovered in the upper and lower horizons of the Wangerrip Group, these horizons being separated by some 800 ft of sediments (Baker 1950, p. 29):

(1) Pebble Point Formation at the base of the Wangerrip Group = Paleocene to Lower Eocene.

(2) Princetown Member and upper portion of the Dilwyn Clay forming the top strata of the Wangerrip Group = Lower Eocene.

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* See Figure 59.

(1) *Paleocene to Lower Eocene.*—Pebble Point Formation, Vic. In addition to the described fauna (Baker 1950, pp. 27, 28) this deposit contains a well-defined microflora (B of Cookson 1954*a*), in which several varieties of pteridophyte and podocarpaceous sporomorphs can be recognized. A number of dicotyledonous pollen types have been observed but the identity of most of them has still to be established. One sporomorph, *Triorites edwardsii* Cookson & Pike, which occurs in several deposits considered as near the base of the Victorian Tertiary sequence, is relatively frequent in the Pebble Point beds.

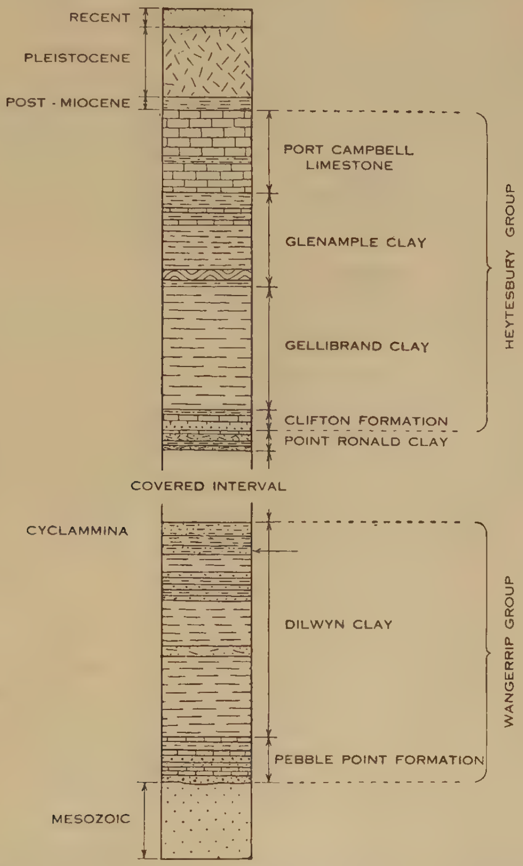
RECENT
PLEISTOCENE
POST - MIOCENE
PORT CAMPBELL LIMESTONE
GLENAMPLE CLAY
GELLIBRAND CLAY
CLIFTON FORMATION
POINT RONALD CLAY
HEYTESBURY GROUP
COVERED INTERVAL
CYCLAMMINA
DILWYN CLAY
PEBBLE POINT FORMATION
WANGERRIP GROUP
MESOZOIC

Fig. 59.—Stratigraphical column showing conformable relationship of *Cyclammina*-bearing carbonaceous sandy sediments to overlying and underlying sediments. Arrow = Princetown Member (*Cyclammina*-bearing). (After Baker 1953, p. 126.)

The microplankton includes:

DINOFLAGELLATA: *Deflandrea bakeri*; *Deflandrea bakeri* f. *pellucida*; *Deflandrea obliquipes*; *Paleoperidinium* sp. plur. indet.; *Eisenackia crassitabulata; Ceratium fusus incerta.*

HYSTRICHOSPHAERIDAE: *Hystrichosphaera* sp. aff. *bulloidea*; *Hystrichosphaeridium heteracanthum; Micrhystridium pachydermum; Micrhystridium* cf. *stellatum*; *Micrhystridium* cf. *inconspicuum*; *Cannosphaeropsis caulleryi.*

PTEROSPERMOPSIDAE: *Pterospermopsis microptera*; *Cymatiosphaera eupeplos.*

LEIOSPHAERIDAE: *Leiosphaera scrobiculata.*

INCERTAE SEDIS: *Epicephalopyxis indentata.*

(2) *Lower Eocene.*—Carbonaceous silty sandstones of the Princetown Member of the Dilwyn Clay, Vic. Macrofossils are scarce in this deposit; specimens of *Cyclammina* (Baker 1953) and a microflora closely similar to that of the Birregurra beds between 760 and 900 ft and to that of the Anglesea sandstone have been identified (Cookson 1954*a*).

The microplankton contains:

DINOFLAGELLATA: *Deflandrea robusta*; *Deflandrea obliquipes*; *Deflandrea pachyceros; Deflandrea* sp.; *Wetzeliella homomorpha*; *Palaeophystrichophora* cf. *spinosissima*; *Eisenackia crassitabulata* (very rare).

HYSTRICHOSPHAERIDAE: *Hystrichosphaera furcata*; *Hystrichosphaera crassipellis*; *Hystrichosphaeridium inodes*; *Hystrichosphaeridium colligerum*; *Micrhystridium* cf. *reticulatum*; ?*Micrhystridium* cf. *ambiguum; Micrhystridium pachydermum; Hystrichokolpoma rigaudae*; *Cannosphaeropsis caulleryi.*

PTEROSPERMOPSIDAE: *Cymatiosphaera* cf. *wetzeli.*

LEIOSPHAERIDAE: *Leiosphaera scrobiculata.*

INCERTAE SEDIS: *Epicephalopyxis indentata.*

(*e*) ?*Middle Eocene**

(i) *Near Mouth of Anglesea River, Vic.*—Black sandstone forming coastal cliffs (Singleton 1941, p. 24). These beds are poorly fossiliferous but in localized areas *Cyclammina* is abundant.

Microflora C (Cookson 1954*a*), which occurs in Birregurra bore and the Princetown Member of the Dilwyn Clay, is well represented.

Included in the microplankton are:

DINOFLAGELLATA INCERTAE SEDIS: *Schematophora speciosa* (very rare).

HYSTRICHOSPHAERIDAE: *Hystrichosphaera ramosa*; *Hystrichosphaeridium inodes*; *Micrhystridium* cf. *ambiguum*; *Hystrichokolpoma rigaudae*; *Cannosphaeropsis caulleryi*; *Cannosphaeropsis urnaformis.*

PTEROSPERMOPSIDAE: *Pterospermopsis microptera.*

INCERTAE SEDIS: *Epicephalopyxis indentata.*

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* Raggatt and Crespin 1952.

(*f*) ? *Lower Eocene*

(i) *Birregurra, Vic., Bore No.* 1.—Black carbonaceous sandstone between 760 and 900 ft. A close palynological correlation has already been established between these beds and the Anglesea sandstone, and the Princetown Member of the Dilwyn Clay (Cookson 1954*a*). Recently Raggatt and Crespin (1952) have placed the Anglesea sandstone in the ? Middle Eocene and Baker (1953) has suggested a Lower Eocene age for the Princetown Member of the Dilwyn Clay. Micropalaeontologically there is no reason why the deposits in this section of the Birregurra bore should not be of approximately the same age. Their microfloras are closely similar and contain, as well as fern spores and coniferous pollen grains, a large number of dicotyledonous types, some of which can be related with a high degree of certainty to living genera.

The microplankton includes:

DINOFLAGELLATA: *Deflandrea phosphoritica.*

DINOFLAGELLATA INCERTAE SEDIS: *Schematophora speciosa.*

HYSTRICHOSPHAERIDAE: *Hystrichosphaera ramosa*; *Hystrichosphaera crassipellis*; *Hystrichosphaeridium inodes*; *Hystrichokolpoma rigaudae*; *Cannosphaeropsis caulleryi*; *Cannosphaeropsis urnaformis.*

PTEROSPERMOPSIDAE: *Cymatiosphaera punctifera*; *Membranilarnax angustivelum; Membranilarnax clathroderma.*

INCERTAE SEDIS: *Epicephalopyxis indentata.*

(*g*) *Miocene or Older*

(i) *Birregurra, Vic., Bore No.* 1.—Dark grey clays at 444-449 and 514-516 ft. The former are poorly fossiliferous and need no further consideration. The sample between 514 and 516 ft, on the other hand, is relatively rich in microfossils. It contains a fair number of Foraminifera, but as far as can be ascertained no correlation has yet been made with a view to establishing the exact age of these beds. Pollen grains and spores occur but no distinctive types have been observed that might link this deposit with the deeper parts of the bore.

The microplankton contains:

DINOFLAGELLATA: *Gymnodinium australiense.*

DINOFLAGELLATA INCERTAE SEDIS: *Schematophora speciosa.*

HYSTRICHOSPHAERIDAE: *Hystrichosphaera furcata*; *Hystrichosphaera ramosa*; *Hystrichosphaera bulloidea*; *Hystrichosphaera hyperacantha*; *Hystrichosphaera borussica*; *Hystrichosphaera cingulata*; *Hystrichosphaeridium centrocarpum*; *Hystrichosphaeridium placacanthum*; *Hystrichosphaeridium machaerophorum*; *Micrhystridium* cf. *inconspicuum*; *Micrhystridium* cf. *ambiguum*; *Hystrichokolpoma rigaudae*: *Cannosphaeropsis urnaformis.*

PTEROSPERMOPSIDAE: *Cymatiosphaera* cf. *wetzeli; Cymatiosphaera eupeplos.*

INCERTAE SEDIS: *Epicephalopyxis indentata.*

(*h*) *Lower Tertiary*

(i) *Near Denmark, W.A.*—"Coffee" rock. Professor R. Prider has kindly informed us that no geological details regarding the age of this deposit are available. On the basis of the contained microflora, which is closely similar to microflora C of the Victorian Eocene deposits, one of us (Cookson 1954*b*) has suggested that it is probably Lower Tertiary in age.

The microplankton preserved in the coffee rock contains several distinctive types not yet met with elsewhere, but holds two in common with eastern Australian Eocene deposits.

DINOFLAGELLATA: *Wetzeliella lineidentata; Palaeohystrichophora* cf. *spinosissima.*

HYSTRICHOSPHAERIDAE: *Hystrichosphaera* cf. *borussica*; *Hystrichosphaeridium floripes*; *Hystrichosphaeridium inodes* subsp. *gracilis.*

PTEROSPERMOPSIDAE: *Pterospermopsis microptera*; *Pterocystidiopsis velata.*

INCERTAE SEDIS: *Epicephalopyxis indentata.*

(*i*) *Upper Eocene or Older*

(i) *Castle Cove Section, Vic.*—Upper Eocene or older is the age suggested by Dr. O. P. Singleton (personal communication) for the basal clays of this section. An Eocene age (possibly Lower to Middle Eocene) is supported by the presence in this deposit of microflora C, previously mentioned as occurring in the Anglesea, Birregurra, and Dilwyn Clay deposits.

In the microplankton the number of individuals and variety of types seem to be rather small, but as yet only a very small sample has been treated. The following forms have been recognized:

DINOFLAGELLATA: *Deflandrea heterophlycta.*

HYSTRICHOSPHAERIDAE: *Hystrichosphaera furcata*; *Cannosphaeropsis caulleryi.*

PTEROSPERMOPSIDAE: *Pterospermopsis microptera.*

INCERTAE SEDIS: *Epicephalopyxis indentata.*

(*j*) *Eocene* (*possibly Lower*)

(i) *Canopus Bore, S.A.*—The samples examined came from between 548 and 574 ft and between 920 and 925 ft. Both contain a large number of spores and pollen grains, the microflora, especially at the deeper levels, being very similar to microflora C of the Victorian Lower Tertiary deposits.

The microplankton is poor in numbers and varieties but three forms, all of which are relatively common in Victorian Eocene deposits, have been observed. They are *Hystrichosphaeridium inodes,* at 920-925 ft; *Hystrichokolpoma rigaudae,* at 548-574 ft; and *Cannosphaeropsis caulleryi,* at 548-574 ft.

(*k*) *Middle Miocene* (*Balcombian*)

(i) *Balcombe Bay and Princetown Districts, Vic.*—Grey marls from Balcombe Bay and the Gellibrand Clay from the Princetown district. These deposits are rich in Foraminifera (Chapman 1907; Chapman and Parr 1926; Chapman, Parr, and Collins 1934) and Mollusca; sclerites are abundant and coccoliths have been recognized during the present study.

The spore and pollen content is low, particularly at the type locality on Balcombe Bay. It includes a few varieties of fern spore, coniferous pollen grains of araucarian and podocarpaceous type, and pollen of *Nothofagus.*

The microplankton includes:

DINOFLAGELLATA: *Gymnodinium australiense* B + P.*

HYSTRICHOSPHAERIDAE: *Hystrichosphaera furcata* B; *Hystrichosphaera ramosa* B; *Hystrichosphaera bulloidea* B + P; *Hystrichosphaera hyperacantha* B; *Hystrichosphaera cingulata* B + P; *Hystrichosphaera borussica* B + P; *Nematosphaeropsis balcombiana* P; *Hystrichokibotium trabeculiferum* B; *Hystrichosphaeridium centrocarpum* B + P; *Hystrichosphaeridium machaerophorum* B + P; *Hystrichosphaeridium placacanthum* B + P; *Micrhystridium* sp. B.

PTEROSPERMOPSIDAE: *Cymatiosphaera eupeplos* B.

(*l*) *Post-Upper Miocene* (*Post-Cheltenhamian*)

(i) *Hampton, Vic.*—A black sandy layer, sometimes exposed at beach level near the Hampton Life Saving Club, is believed by its discoverer, Mr. H. T. Clifford, to be post-Cheltenhamian in the Victorian Tertiary sequence of Singleton (1941, p. 32), i.e. post-Upper Miocene.

The bed contains numerous pollen grains, including *Nothofagus,* but the exact composition of the microflora has not been determined.

No dinoflagellates have been observed but several unclassified types of hystrichospheres occur in the preparations. The most distinctive and interesting type has been described under the name *Hystrichosphaeridium choanophorum.*

VII. Stratigraphical Remarks

In spite of the preliminary character of the present work some of the results obtained are worthy of immediate consideration in relation to both local and general stratigraphy. It should be mentioned, however, that although the absence of individual microfossils from a deposit may, if cautiously considered, give useful indications,* it is their presence and not their absence that is of real stratigraphical value.

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* B refers to the Balcombe Bay locality and P to the Balcombian deposit near Princetown, Vic.

(a) *Local Stratigraphical Correlations*

Some of the Australian samples, for example, those from the Upper Cretaceous (Senonian) of Gingin and the Middle Miocene of Balcombe Bay, are well dated and thus useful in correlations with undated samples from bores. The age of others, such as the Lower Cretaceous sample from Onepah Station and the Paleocene to Lower Eocene Pebble Point Formation, is less certain. Two Victorian bores, the Nelson and the Birregurra bores, may be usefully cited in this connexion.

(i) *Nelson Bore.*—Three levels can be considered, the first, comprising the deepest samples examined, at 6192-5782 ft, the second at 3874 ft, and the third at 992 ft.

Between 6192 and 5782 ft the presence of *Hystrichosphaeridium complex, H. heteracanthum,* and *Odontochitina cribropoda* has been established. All of these forms occur in the Upper Cretaceous of Gingin, W.A. The genotype *Odontochitina operculata* of the European Upper Cretaceous has been found in the Lower Cretaceous of Onepah Station and from the Era River, Papua, New Guinea, but has not been identified in any of the Tertiary residues.

In the deposit at 3874 ft *H. heteracanthum* is accompanied by *Deflandrea bakeri* f. *pellucida.* This form, like *D. bakeri* typica, is common in the Pebble Point Formation (Paleocene to Lower Eocene).

At 992 ft, *Epicephalopyxis indentata* has been recognized. This form is relatively common in the upper and lower strata of the Wangerrip Group and related Australian Older Tertiary deposits, but it is apparently absent from Australian Cretaceous sediments. The microfloral assemblage (microflora C of Cookson 1954*a*) at 992 ft is comparable with that of the upper part of the Wangerrip Group (Lower Eocene). Thus the ages of these three levels in the Nelson Bore appear to be Upper Cretaceous, Paleocene to Lower Eocene, and Lower Eocene respectively.

(ii) *Birregurra Bore No.* 1.—Table 1 compares the microplankton assemblages found at two levels of this bore and other Australian Older Tertiary and Miocene deposits.

The lower level, i.e. between 760 and 960 ft, has several important types in common with sediments at the Lower Eocene localities specified, all of which appear to be closely related to one another at least as far as their phytoplankton content is concerned.

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* The absence of *Hystrichosphaeridium tubiferum,* taken in the wide sense, from Australian Tertiary deposits is noticeable since this type, well represented by *H. complex, H. recurvatum,* and *H. pulcherrimum,* is frequent in Australian Cretaceous beds.

The higher level (444-516 ft), at which several of the lower-level types still persist, also contains a series of species which are relatively abundant in Balcombian deposits (Middle Miocene) but so far have not been recognized in Lower Tertiary sediments.

TABLE 1

DISTRIBUTION OF SOME OF THE COMPONENTS OF THE PHYTOPLANKTON IN OLDER TERTIARY AND MIOCENE DEPOSITS OF SOUTHERN AUSTRALIA

Species	Lower Eocene to Paleocene	Lower Eocene	Eocene					Miocene or Older	Miocene
	Pebble Point Formation, Vic.	Princetown Member of Dilwyn Clay, Vic.	Birregurra Bore, Vic., 760-960 ft.	Anglesea, Vic.	Castle Cove, Vic.	Canopus Bore, S.A.	Near Denmark, W.A.	Birregurra Bore, Vic., 514-516 ft.	Balcombian: Balcombe Bay, Vic.
Gymnodinium australiense	—	—	—	—	—	—	—	+	+
Deflandrea bakeri	+	—	—	—	—	—	—	—	—
Deflandrea phosphoritica	—	—	+	—	—	—	—	—	—
Deflandrea spec. plu.	+	+	—	—	—	—	—	—	—
Deflandrea heterophlycta	—	—	—	—	+	—	—	—	—
Eisenackia crassitabulata	+	+	—	—	—	—	—	—	—
Schematophora speciosa	—	—	+	+	—	—	—	+	—
Hystrichosphaera crassipellis	—	+	+	—	—	—	—	—	—
Hystrichosphaera furcata	—	+	—	—	+	—	—	+	+
Hystrichosphaera ramosa	—	—	—	+	—	—	—	+	+
Hystrichosphaera bulloidea	—	—	—	—	—	—	—	+	+
Hystrichosphaera hyperacantha	—	—	—	—	—	—	—	+	+
Hystrichosphaera cingulata	—	—	—	—	—	—	—	+	+
Hystrichosphaera borussica	—	—	—	—	—	—	+	+	+
Hystrichosphaeridium centrocarpum	—	—	—	—	—	—	—	+	+
Hystrichosphaeridium placacanthum	—	—	—	—	—	—	—	+	+
Hystrichosphaeridium machaerophorum	—	—	—	—	—	—	—	+	+
Hystrichosphaeridium inodes	—	+	+	+	—	+	+	—	—
Hystrichokolpoma rigaudae	—	+	+	+	—	+	—	+	—
Cannosphaeropsis caulleryi	+	+	+	+	—	—	—	—	—
Cannosphaeropsis urnaformis	—	—	+	+	—	—	—	+	—
Pterospermopsis microptera	+	—	—	+	+	—	+	—	—
Epicephalopyxis indentata	+	+	+	+	+	—	+	+	—

(*b*) *General Stratigraphical Implications*

From the point of view of general stratigraphy the results already obtained are of considerable interest. In the first place, there is a noticeable number of European genera and species in Australian deposits. Of the 25 genera recorded here only four are new. One of these, *Cyclonephelium*, is also present in Europe. The other three, *Eisenackia*, *Schematophora*, and *Nematosphaeropsis*, are from the Tertiary, but unlike the European Palaeozoic and Mesozoic this period has not yet been made the subject of extensive microplanktonic research. It is therefore quite possible that these genera will ultimately be found in the northern hemisphere. The number of new species is proportionately greater, viz. almost 60 per cent. of the collection and more than 78 per cent. for the Tertiary alone.

Of the European Cretaceous dinoflagellates found in Australia the genera *Hystrichodinium* and *Dinopterygium* are of special interest.

Hystrichodinium oligacanthum from the Onepah Station deposit is quite distinct from *H. pulchrum* and its varieties in the European Senonian. In France the genus *Hystrichodinium* seems to be restricted to the Upper Cretaceous and is not known below the Turonian horizon. If the age of the Onepah sample is confirmed it will show that this genus appeared earlier in the southern hemisphere.

The same apparent precocity is seen also in two other genera, *Deflandrea* amongst the dinoflagellates and *Cyclonephelium* amongst the Hystrichosphaeridae.

In Australia *Deflandrea* first appears in the Pebble Point Formation (Paleocene to Lower Eocene). In Europe it has been recorded from the Ypresian (Lower Eocene) of Belgium (Pastiels 1948; Reissinger 1950), but has not been seen in the Landenian. It is in the Upper Eocene (Klumpp 1953) and in the Oligocene (Eisenack 1954) that the genus is most frequent.

The genus *Cyclonephelium* is well represented in the Australian Cretaceous but has not been found in any of the Tertiary deposits examined. This genus is still unknown from European Cretaceous flints although its complete absence cannot be affirmed. However, according to the descriptions and figures of two of Pastiels' organisms upon which our two new species *Cyclonephelium exuberans* and *C. pastielsi* have been based (this paper, page 285), this genus is present in the Ypresian of Belgium. It thus seems possible that *Cyclonephelium* appeared earlier in the southern (Lower and Upper Cretaceous) than in the northern hemisphere (Lower Eocene).

Dinopterygium cladoides, which in Europe has been found in Cretaceous and Lower Eocene deposits,* is another type that seems to have appeared later in European than in Australian deposits. When it is realized that in the Onepah assemblage there are eight or nine types (*D. cladoides, Hystrichosphaera furcata, H. speciosa, H. wetzeli, Hystrichosphaeridium complex, H. pulcherrimum, H. recurvatum, Odontochitina operculata*) common to European Upper Cretaceous sediments, it seems reasonable to regard the age of the Onepah sample as either Upper or Lower Cretaceous. However, later research should solve this problem.

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* "Peridinales" sec. Reissinger, 1950, p. 19, fig. 11.

Another interesting point is the persistence of several European Jurassic types in younger Australian deposits. *Cannosphaeropsis aemula* of the Oxfordian (Upper Jurassic) of France has been found in the Lower Cretaceous of New Guinea and another Oxfordian type, *C. caulleryi*, occurs frequently in Victorian Older Tertiary deposits.

Hystrichosphaeridium polytrichum of the French Bathonian (Middle Jurassic) exists in the Upper Cretaceous of Gingin. Another representative of the European Jurassic, *Cymatiosphaera eupeplos*, has been observed in Australian Cretaceous, Eocene, and Miocene deposits.

Several European species occur in Australian deposits of approximately similar ages. Among these *Gymnodinium heterocostatum, Hystrichosphaera ramosa, Hystrichosphaeridium complex, H. recurvatum*, and *H. flosculus* occur in the Upper Cretaceous, while *Deflandrea phosphoritica, Wetzeliella homomorpha, Hystrichosphaera borussica, Hystrichosphaeridium inodes, H.* cf. *tiara, Cymatiosphaera* cf. *wetzeli*, and *C. eupeplos* occur in the Older Tertiary.

It is more difficult to give an idea of the forms which may eventually prove to be endemic. Of the large number of genera of Protista in the marine plankton, the greater number of species are cosmopolitan, but some genera and a certain number of species and varieties have a special distribution and live in limited areas, some in warm waters, others in cold. It is therefore not impossible that the fossil microplanktonic assemblages may contain some species with restricted distributions.

In the Australian Cretaceous, *Hystrichosphaeridium isocalamus* and more especially *H. striatoconus* (frequent at Gingin) may be mentioned as quite distinct from all of the known European hystrichosphaerids. In Europe Tertiary forms are still incompletely known; nevertheless the Australian forms *Hystrichosphaeridium floripes, H. colligerum*, and perhaps *Hystrichokolpoma rigaudae* appear to belong to the special area studied here.

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EXPLANATION OF PLATES 1-9*

PLATE 1

Fig. 1.—*Hystrichodinium oligacanthum* sp. nov. Paratype. Front view. Onepah Station, N.S.W. × 385. P16208.†

Fig. 2.—*Dinopterygium cladoides* Defl. Hypotype. Polar view. Onepah Station, N.S.W. × *c.* 400. P16210.

Fig. 3.—*Gonyaulax* cf. *wetzeli* Lej.-Carp. Oblique view. Onepah Station, N.S.W. × 540. P16208.

Fig. 4.—*Palaeoglenodinium* sp. indet. Part of a theca showing the transverse girdle on the right-hand side. Gingin, W.A. × 413. P16211.

Fig. 5.—*Palaeohystrichophora multispina* sp. nov. Holotype. Front view. Gingin, W.A. × 576. P16212.

Fig. 6.—*Gonyaulax* sp. indet. Onepah Station, N.S.W. × 400. P16210.

Fig. 7.—*Gymnodinium* cf. *heterocostatum* Defl. Gingin, W.A. × 425. P16213.

Fig. 8.—*Hystrichosphaeridium pulcherrimum* sp. nov. Holotype. Onepah Station, N.S.W. × 447. P16214.

Figs. 9, 10.—*Hystrichosphaeridium complex* (White) Defl. Hypotypes. × 418.
Fig. 9.—Gingin, W.A. P16215. Fig. 10.—Onepah Station, N.S.W. P16208.

Figs. 11, 12.—*Hystrichosphaeridium recurvatum* (White) Defl. Hypotypes. × 460.
Fig. 11.—Gingin, W.A. P16211. Fig. 12.—Small form from Onepah Station, N.S.W. × 400. P16216.

PLATE 2

Fig. 1.—*Hystrichosphaera ramosa* (Ehr.) O. Wetzel. Gingin, W.A. Hypotype. × *c.* 400. P16217.

Fig. 2.—*Hystrichosphaeridium polytrichum* Val. Hypotype. Gingin, W.A. × 440. P16213.

Fig. 3.—*Hystrichosphaeridium flosculus* Defl. Hypotype. Gingin, W.A. × 400. P16218.

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* All the photographs are from untouched negatives. For the photographs shown in Plate 1, Figure 4, Plate 2, Figures 5, 8, and 14, and Plate 3, Figure 4, we are indebted to Mr. E. Ashby, Barker Cryptogamic Research Laboratory, University of Manchester.

† References so given are the registered numbers in the palaeontological collection of the National Museum of Victoria.

Fig. 4.—*Hystrichosphaeridium fimbriatum* (White) Defl. Hypotype. Onepah Station, N.S.W. × *c.* 570. P16210.

Fig. 5.—*Hystrichosphaeridium heteracanthum* sp. nov. Holotype Nelson Bore, Vic., at 6065 ft. × 400. P16219.

Fig. 6.—*Hystrichosphaeridium heteracanthum.* Paratype. Another example to show the short, broad type of process. Nelson Bore, Vic., at 5782 ft. × 400. P16220.

Figs. 7, 8.—*Hystrichosphaeridium isocalamus* sp. nov. Holotype. Two views of the holotype. Onepah Station, N.S.W. × 600. P16221.

Fig. 9.—*Hystrichosphaeridium salpingophorum* Defl. Hypotype. Era River, Papua, N.G. × 424. P16222.

Fig. 10.—*Hystrichosphaeridium striatoconus* sp. nov. Paratype. Gingin, W.A. × 426. P16218.

Fig. 11.—*Cyclonephelium compactum* sp. nov. Paratype. Gingin, W.A. × *c.* 425. P16223.

Fig. 12.—*Cyclonephelium compactum.* Holotype and genotype. Onepah Station, N.S.W. × 420. P16224.

Fig. 13.—*Cyclonephelium compactum.* Paratype. Another specimen. Onepah Station, N.S.W. × 535. P16225.

Fig. 14.—*Cyclonephelium distinctum* sp. nov. Holotype. Gingin, W.A. × 400. P16218.

PLATE 3

Fig. 1.—*Cannosphaeropsis aemula* Defl. Hypotype. Era River district, Papua, N.G. × 290. P16226.

Fig. 2.—*Cannosphaeropsis fenestrata* sp. nov. Holotype. Gingin, W.A. × 420. P16227.

Fig. 3.—*Leiosphaera scrobiculata* sp. nov. Holotype. Gingin, W.A. × 400. P16228.

Fig. 4.—*Pterospermopsis australiensis* sp. nov. Holotype. Onepah Station, N.S.W. × 600. P16221.

Fig. 5.—*Odontochitina operculata* Defl. Hypotype. Inferior part. Onepah Station, N.S.W. × 435. P16229.

Fig. 6.—*Odontochitina operculata.* Hypotype. Onepah Station, N.S.W. × *c.* 200. P16230.

Fig. 7.—*Odontochitina cribropoda* sp. nov. Holotype. An almost complete specimen, body badly folded. Nelson Bore, Vic., at 5782 ft. × *c.* 400. P16231.

Fig. 8.—*Odontochitina cribropoda.* Paratype. Specimen used in reconstruction shown in Fig. 58 (text). Nelson Bore, Vic., at 5782 ft. × 195. P16232.

Fig. 9.—*Odontochitina cribropoda.* Paratype. Inferior part. Gingin, W.A. × 200. P16213.

Fig. 10.—*Odontochitina cribropoda.* One of the appendages of previous specimen. × 600. P16213.

Fig. 11.—*Odontochitina cribropoda.* Paratype. A single appendage. Nelson Bore, Vic., at 5782 ft. × 600. P16233.

Fig. 12.—*Epicephalopyxis spectabilis* sp. nov. Paratype. Era River district, Papua, N.G. × 400. P16234.

Fig. 13.—*Epicephalopyxis spectabilis.* Paratype. Era River district, Papua, N.G. × 600. P16235.

Fig. 14.—*Epicephalopyxis spectabilis.* Holotype. Era River, Papua, N.G. × 416. P16235.

PLATE 4

Fig. 1.—*Deflandrea bakeri* sp. nov. Holotype from the front. Pebble Point Formation. × 600. P16236.

Fig. 2.—*Deflandrea bakeri.* Another specimen from Pebble Point Formation. × 600. Deflandre collection, BX36.

Fig. 3.—*Deflandrea bakeri* forma *pellucida* f. nov. Holotype of form. Nelson Bore, Vic., at 3874 ft. × 428. P16237.

Fig. 4.—*Deflandrea bakeri.* The specimen shown in Plate 4, Figure 2, in lateral view. × 400.

Fig. 5.—*Deflandrea phosphoritica* Eis. Hypotype. Birregurra, Vic., bore No. 1 at 876-877 ft. × *c.* 400. P16238.

Fig. 6.—*Deflandrea obliquipes* sp. nov. Holotype. Princetown Member of Dilwyn Clay, Vic. × *c.* 400. P16239.

Fig. 7.—*Deflandrea pachyceros* sp. nov. Holotype. Princetown Member of Dilwyn Clay, Vic. × *c.* 400. P16240.

Fig. 8.—*Deflandrea* sp. Princetown Member of Dilwyn Clay, Vic. × *c.* 600. P16241.

Fig. 9.—*Deflandrea robusta* sp. nov. Holotype. Princetown Member of Dilwyn Clay, Vic. × 440. P16242.

Fig. 10.—*Palaeohystrichophora* cf. *spinosissima* Defl. Hypotype. Princetown Member of Dilwyn Clay, Vic. × 385. P16243.

PLATE 5

Fig. 1.—*Gymnodinium australiense* sp. nov. Holotype. Balcombe Bay, Vic. × 615. P16244.

Fig. 2.—*Eisenackia crassitabulata* sp. nov. Holotype and genotype. Pebble Point Formation, Vic. × *c.* 600. P16245.

Figs. 3, 4.—*Hystrichosphaera bulloidea* sp. nov. Surface view and optical section of holotype from Balcombe Bay, Vic. × 400. P15654.

Fig. 5.—*Wetzeliella lineidentata* sp. nov. Holotype. Near Denmark, W.A. × 385. P16246.

Fig. 6.—*Deflandrea heterophlycta* sp. nov. Paratype. An isolated cyst. Castle Cove, Vic. × 420. P16247.

Fig. 7.—*Wetzeliella homomorpha* sp. nov. Holotype. Princetown Member of Dilwyn Clay, Vic. × 400. P15640.

Fig. 8.—*Hystrichosphaera ramosa* (Ehr.) O. Wetzel. Hypotype. Balcombe Bay, Vic. × 425. P16248.

Fig. 9.—*Hystrichosphaera borussica* Eis. Hypotype. Balcombe Bay, Vic. × 574. P16249.

Fig. 10.—*Hystrichosphaera* cf. *borussica.* Near Denmark, W.A. × 588. P16250.

Figs. 11, 12.—*Micrhystridium* cf. *reticulatum* Defl. Surface view and optical section of the same specimen (figured in *Mem. Nat. Mus., Melb.* 18: Plate 2, Figs. 31-32). Princetown Member of Dilwyn Clay, Vic. × 400.

PLATE 6

Fig. 1.—*Hystrichosphaera ramosa* (Ehr.) O. Wetzel. Hypotype. Specimen focused to show equatorial fields. Balcombe Bay, Vic. × 430. P16292.

Fig. 2.—*Hystrichosphaera crassipellis* sp. nov. Holotype. Princetown Member of Dilwyn Clay, Vic. × 420. P16240.

Fig. 3.—*Hystrichosphaera crassipellis.* Portion of same specimen showing sculpture of shell membrane. × 840.

Figs. 4, 5.—*Hystrichosphaera cingulata* (O. Wetzel) Defl. Hypotype. Surface view and optical section of the one specimen. Balcombe Bay, Vic. × 570. P16293.

Fig. 6.—*Hystrichokolpoma rigaudae* sp. nov. Holotype. Birregurra, Vic., bore No. 1 at 514-516 ft. × 440. P16294.

Fig. 7.—*Hystrichosphaera hyperacantha* sp. nov. Holotype. Balcombe Bay, Vic. × *c.* 420. P16244.

Fig. 8.—*Pterospermopsis microptera* sp. nov. Holotype. Castle Cove, Vic. × 555. P16295.

Fig. 9.—*Cymatiosphaera eupeplos* (Val.) Defl. Hypotype. Balcombe Bay, Vic. × 1600. P16407.

Fig. 10.—*Hystrichokolpoma rigaudae* sp. nov. Paratype. Birregurra, Vic., bore No. 1 at 760-761 ft. × 740. P16296.

Figs. 11, 12.—*Schematophora speciosa* sp. nov. Holotype and genotype. Upper and lower surface of holotype. Birregurra, Vic., bore No. 1 at 842-843 ft. × *c.* 550. P16297.

Fig. 13.—*Schematophora speciosa.* Paratype. Birregurra, Vic., bore No. 1 at 833-834 ft. × 588. P16298.

PLATE 7

Fig. 1.—*Hystrichosphaeridium floripes* sp. nov. Holotype. Near Denmark, W.A. × 350. P16299.

Fig. 2.—*Hystrichosphaeridium floripes.* Paratype. Portion of another specimen. Near Denmark, W.A. × 366. P16300.

Fig. 3.—*Hystrichosphaeridium colligerum* sp. nov. Holotype. Princetown Member of Dilwyn Clay, Vic. × 870. P16301.

Fig. 4.—*Membranilarnax angustivelum* sp. nov. Holotype. Birregurra, Vic., bore No. 1 at 794-795 ft. × 575. P16302.

Fig. 5.—*Membranilarnax angustivelum.* Paratype. Birregurra, Vic., bore No. 1 at 791-792 ft. × *c.* 600. P16303.

Fig. 6.—*Membranilarnax clathroderma* sp. nov. Holotype. Birregurra, Vic., bore No. 1 at 842-843 ft. × 800. P16304.

Fig. 7.—*Hystrichosphaeridium floripes.* A single appendage. Near Denmark, W.A. × 400.

Fig. 8.—*Cannosphaeropsis caulleryi* Defl. Hypotype. Dilwyn Clay, Vic. × 424. P16305.

Figs. 9, 10.—*Cannosphaeropsis urnaformis* Cookson. Surface view and optical section of the holotype. Anglesea, Vic. × 400. P15637.

Fig. 11.—*Schematophora speciosa* sp. nov. Paratype. Birregurra, Vic., bore No. 1 at 876-877 ft. × 573. P16306.

Fig. 12.—Hystrichosphaeridae vel Dinoflagellata. Onepah Station, N.S.W. × *c.* 600. P16210.

Fig. 13.—*Hystrichosphaeridium* cf. *tiara* Klumpp. Anglesea, Vic. × 330. P16307.

Fig. 14.—*Cymatiosphaera punctifera* sp. nov. Holotype. Birregurra, Vic., bore No. 1 at 837-838 ft. × 1130. P16308.

PLATE 8

Fig. 1.—?*Ceratium* cf. *fusus* forma *incerta* Defl. Pebble Point Formation, Vic. × 555. P16236.

Fig. 2.—*Micrhystridium* cf. *ambiguum* Defl. Anglesea, Vic. × 400. P15635.

Figs. 3, 4.—*Hystrichosphaeridium centrocarpum* sp. nov. Surface view and optical section of the holotype. Balcombe Bay, Vic. × 400. P15654.

Fig. 5.—*Nematosphaeropsis balcombiana* sp. nov. Holotype and genotype. Gellibrand Clay, Princetown, Vic. × 820. P16309.

Fig. 6.—*Hystrichokibotium trabeculiferum* sp. nov. Holotype. Balcombe Bay, Vic. × *c.* 700. P16249.

Fig. 7.—*Hystrichosphaeridium inodes* Klumpp. Hypotype. Princetown Member of Dilwyn Clay, Vic. × 660. P16301.

Fig. 8.—*Pteridocystidiopsis velata* sp. nov. Holotype. Near Denmark, W.A. × 363. P16246.

Fig. 9.—*Hystrichosphaera furcata* (Ehr.) O. Wetzel. Hypotype. Balcombe Bay, Vic. × *c.* 500. P16249.

Fig. 10.—*Hystrichosphaera speciosa* Defl. Hypotype. Onepah Station, N.S.W. × *c.* 550. P16214.

PLATE 9

Figs. 1, 2.—*Hystrichosphaeridium placacanthum* sp. nov. Surface view and optical section of holotype. Balcombe Bay, Vic. × 560. P16310.

Fig. 3.—*Hystrichosphaeridium placacanthum.* Balcombe Bay, Vic. × *c.* 560.

Figs. 4, 8.—*Hystrichosphaeridium machaerophorum* sp. nov. Two specimens (Fig. 4, holotype). Balcombe Bay, Vic. × 535. P16312.

Fig. 5.—*Epicephalopyxis indentata* sp. nov. Castle Cove, Vic. × 600.

Fig. 6.—*Epicephalopyxis indentata.* Holotype. Birregurra, Vic., at 959-960 ft. × 409. P16360.

Fig. 7.—*Epicephalopyxis indentata.* A small portion of indented margin of shell. Princetown Member of Dilwyn Clay, Vic. × 600.

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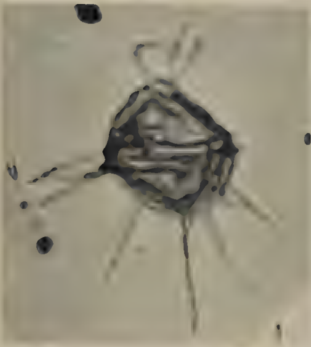
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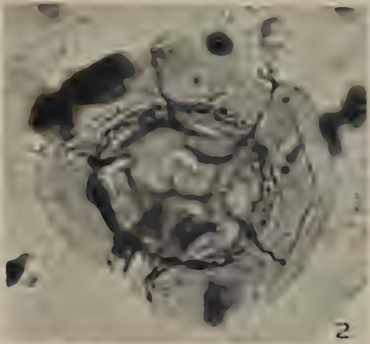
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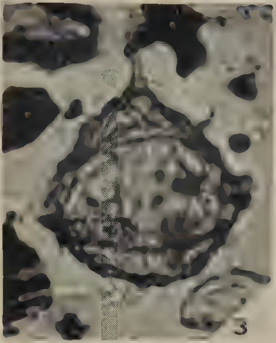
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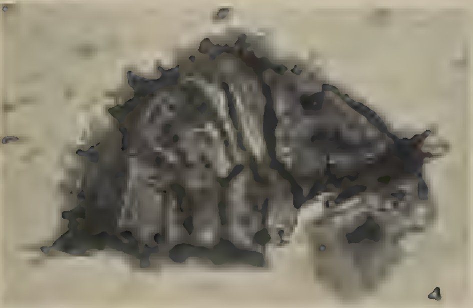
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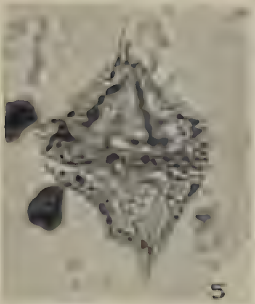
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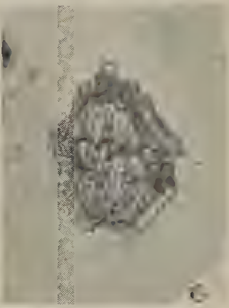
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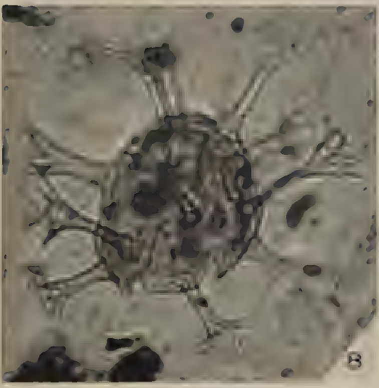
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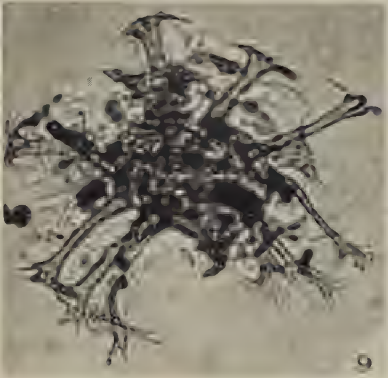
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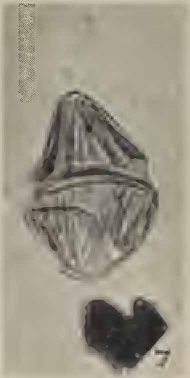
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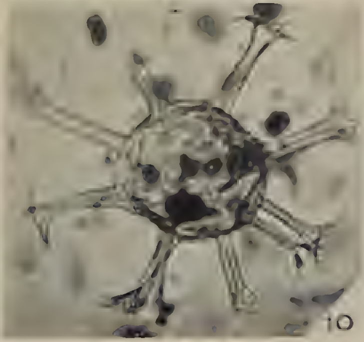
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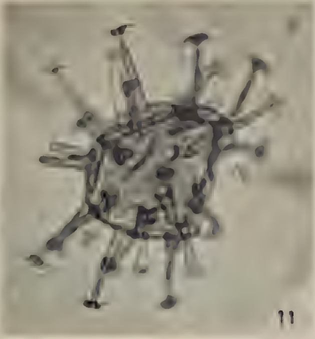
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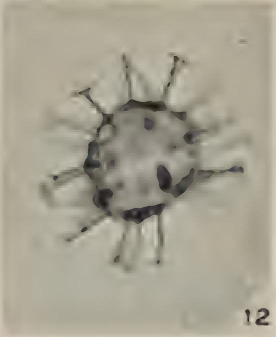
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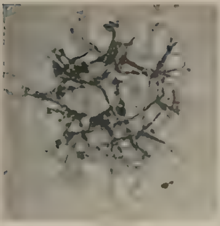
FOSSIL MICROPLANKTON FROM AUSTRALIAN SEDIMENTS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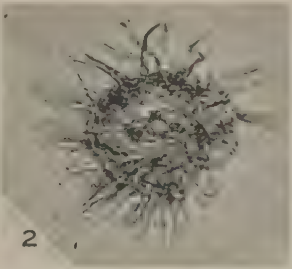
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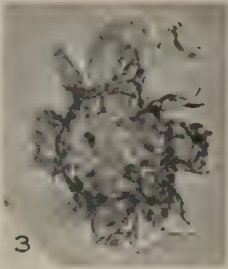
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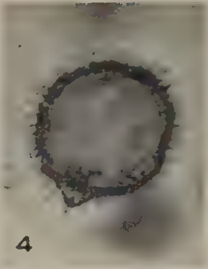
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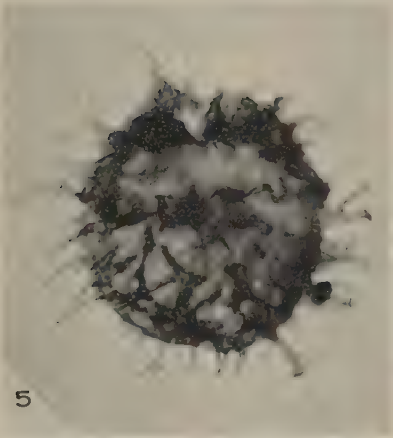
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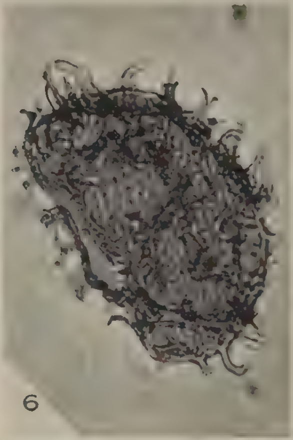
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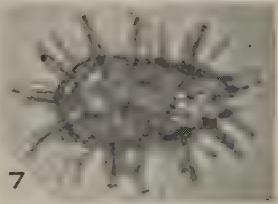
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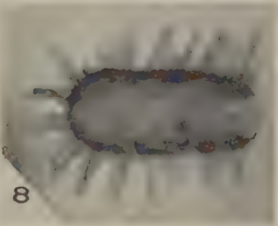
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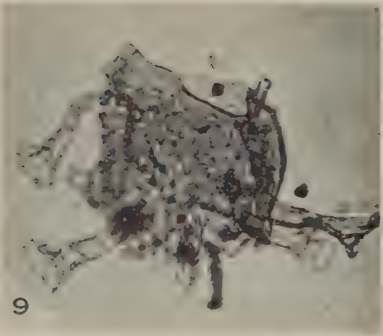
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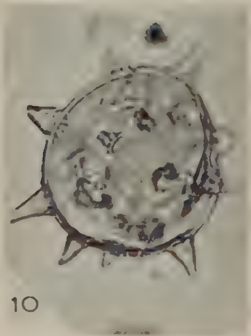
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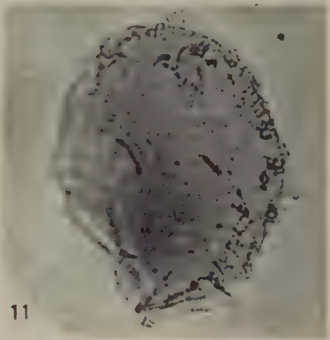
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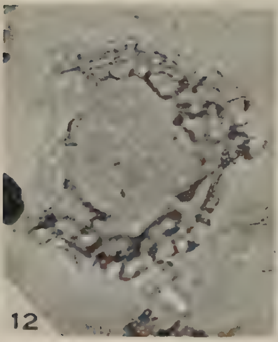
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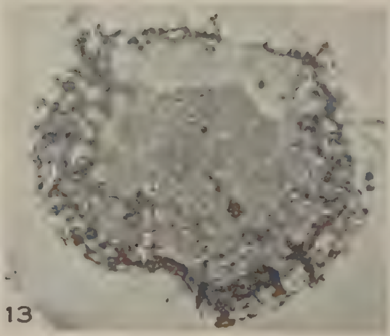
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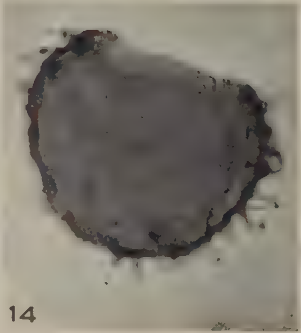
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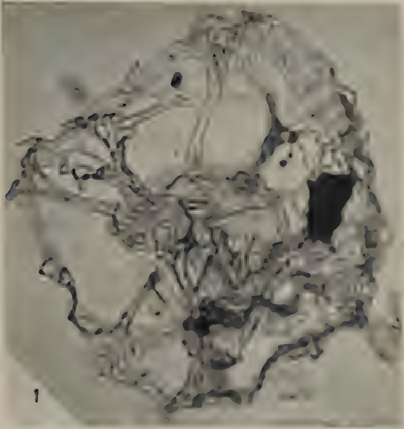
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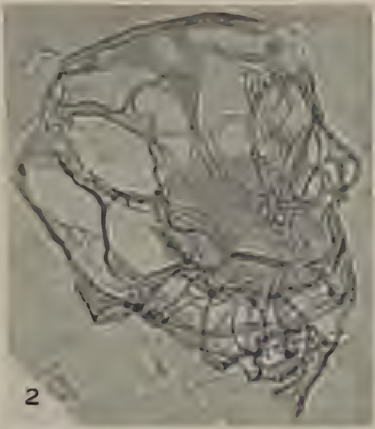
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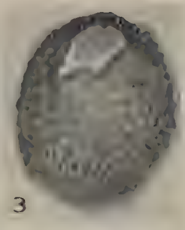
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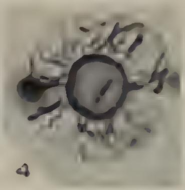
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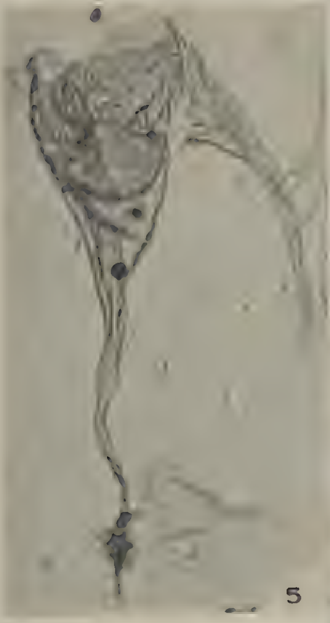
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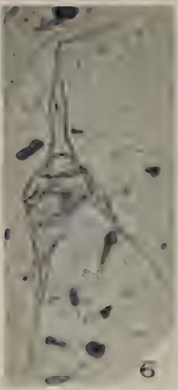
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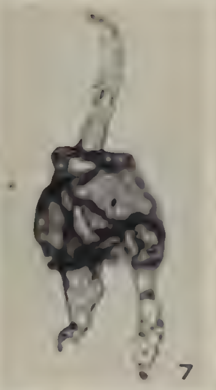
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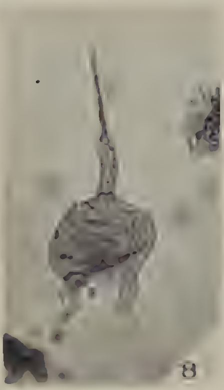
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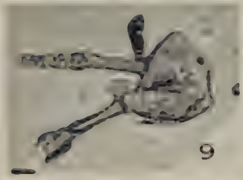
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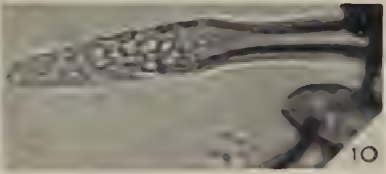
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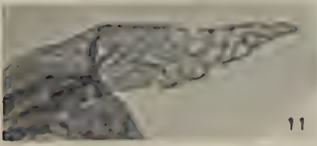
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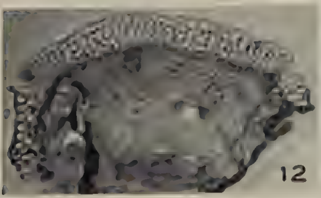
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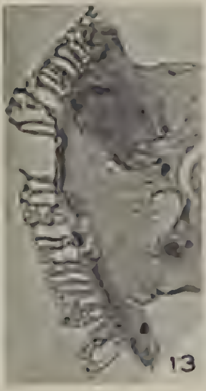
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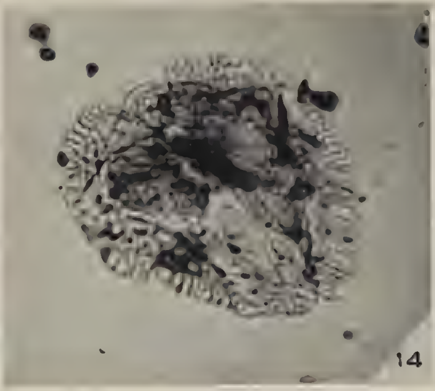
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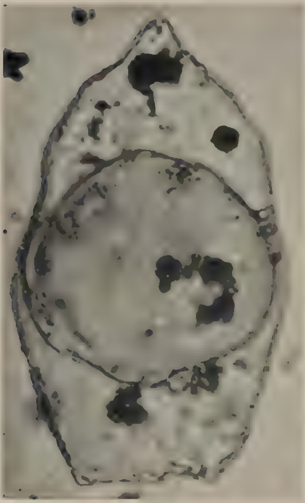

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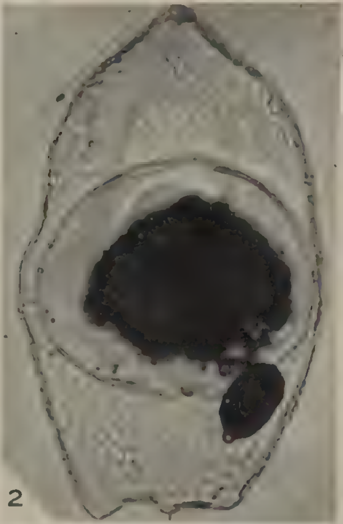

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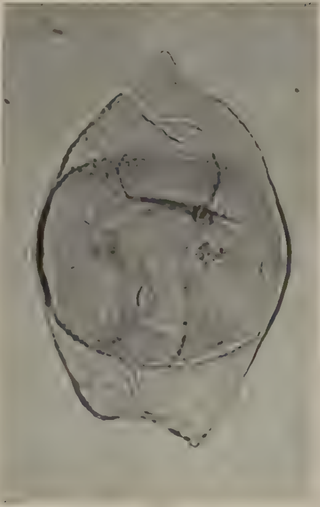

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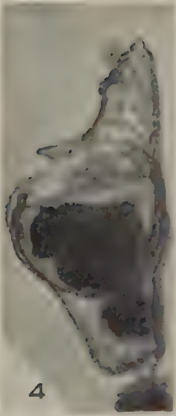

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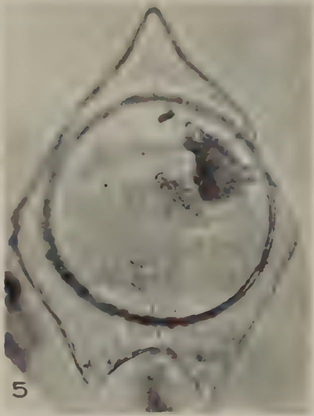

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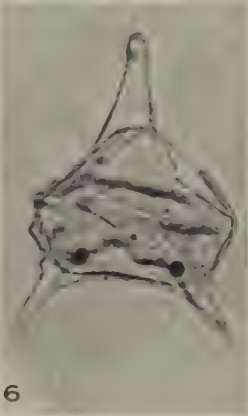

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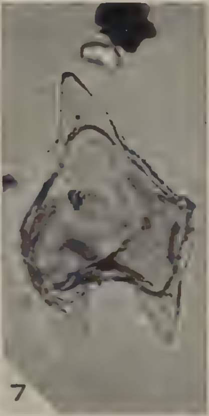

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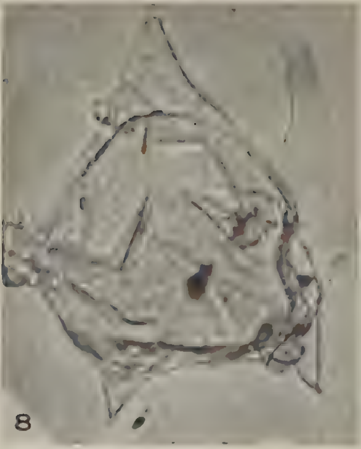

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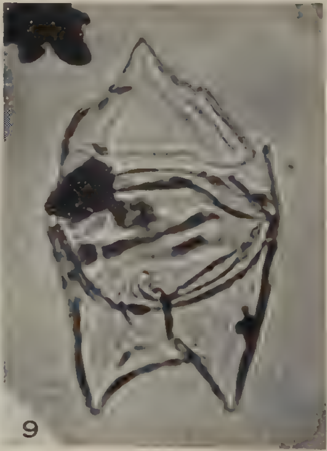

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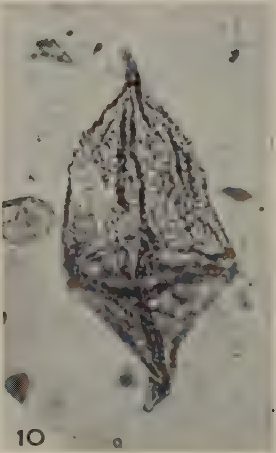

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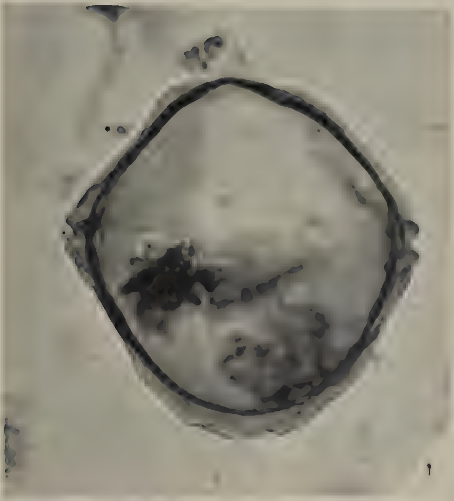
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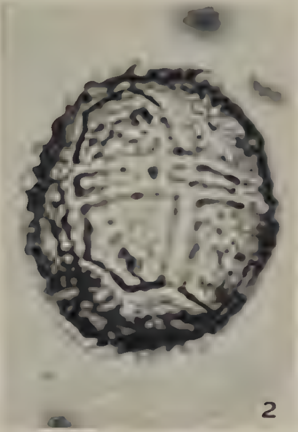
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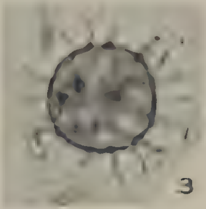
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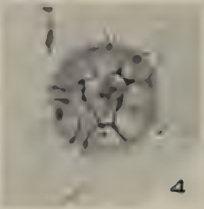
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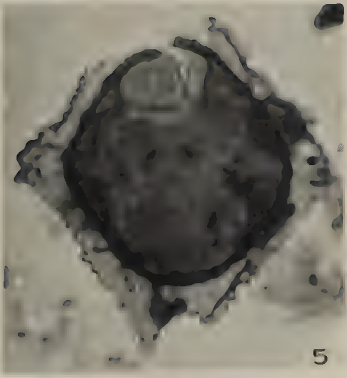
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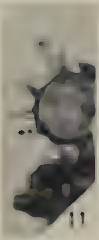
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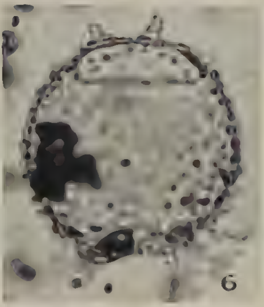
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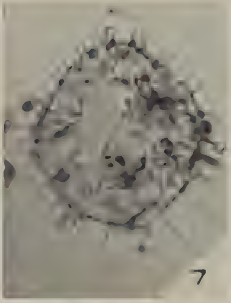
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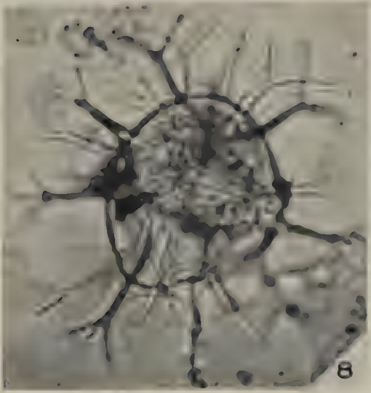
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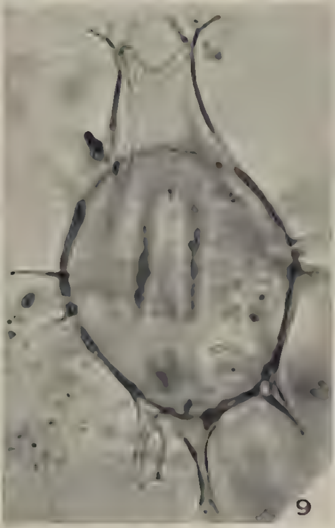
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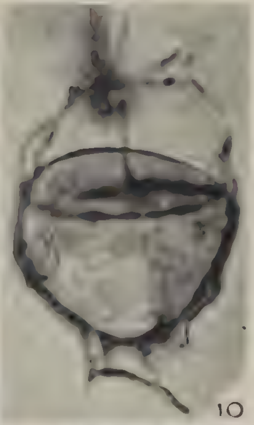
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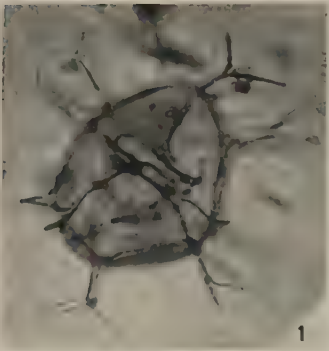
FOSSIL MICROPLANKTON FROM AUSTRALIAN SEDIMENTS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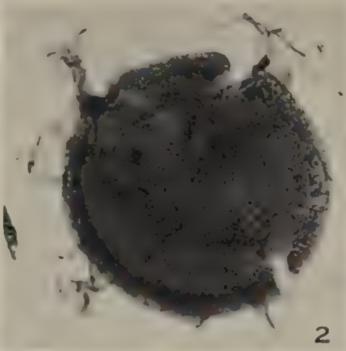
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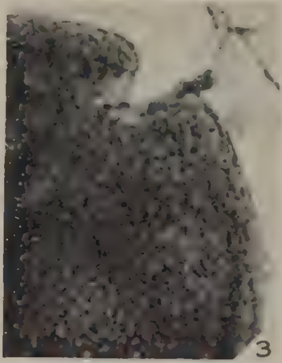
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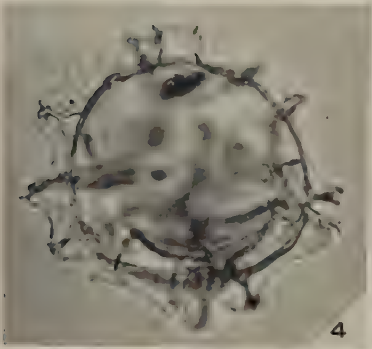
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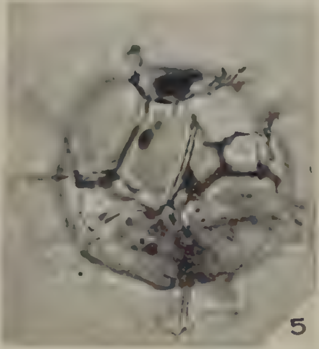
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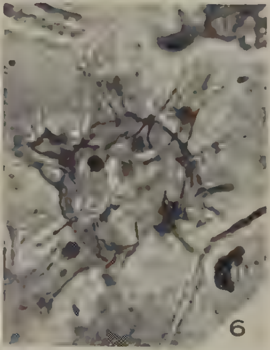
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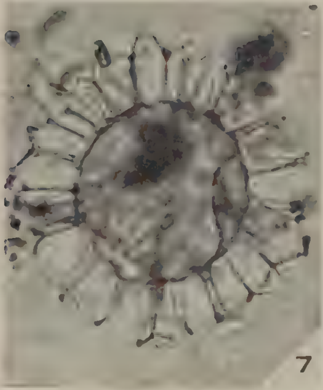
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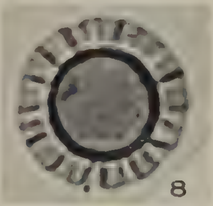
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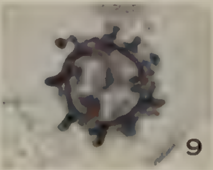
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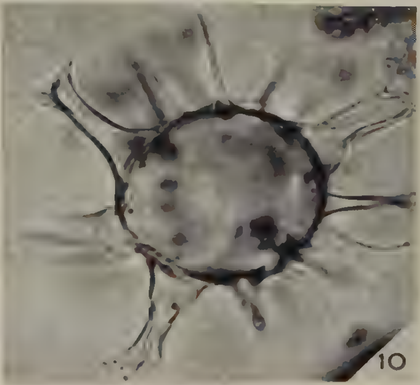
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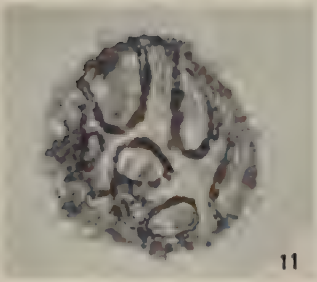
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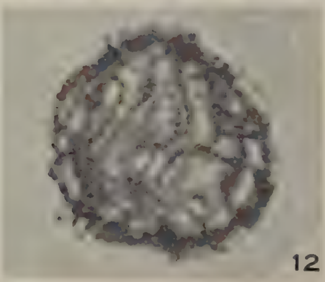
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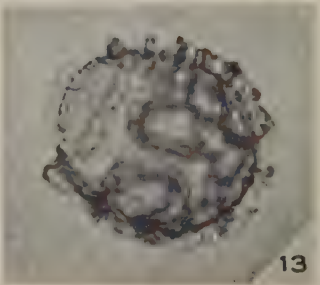
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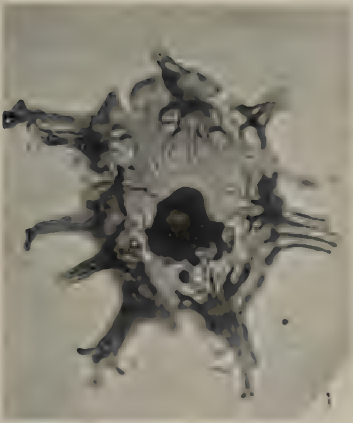
FOSSIL MICROPLANKTON FROM AUSTRALIAN SEDIMENTS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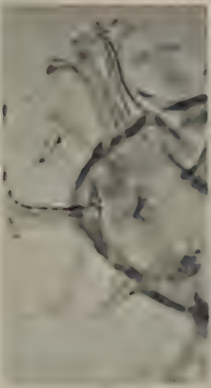
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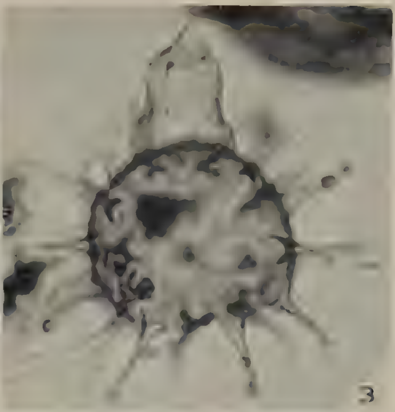
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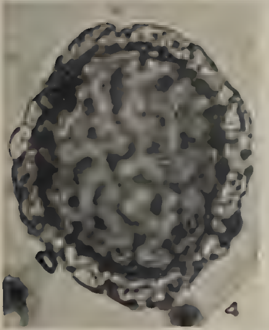
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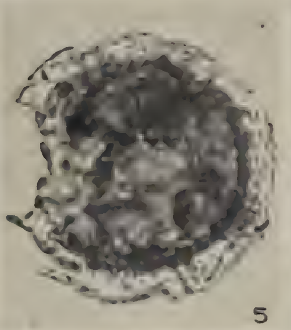
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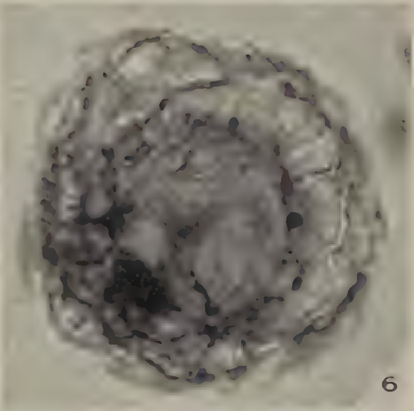
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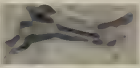
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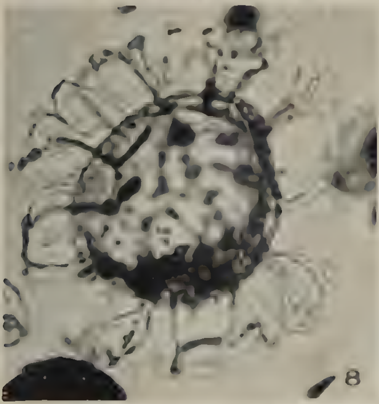
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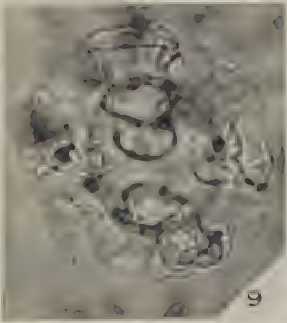
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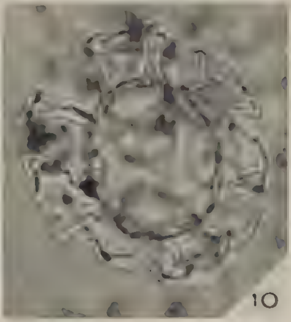
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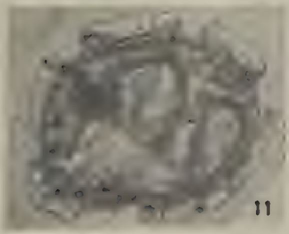
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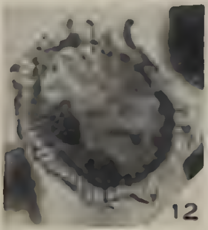
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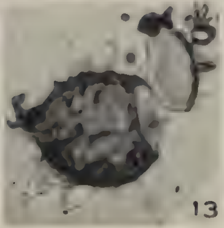
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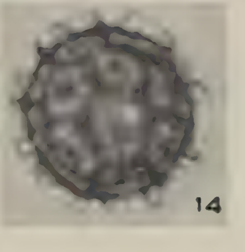
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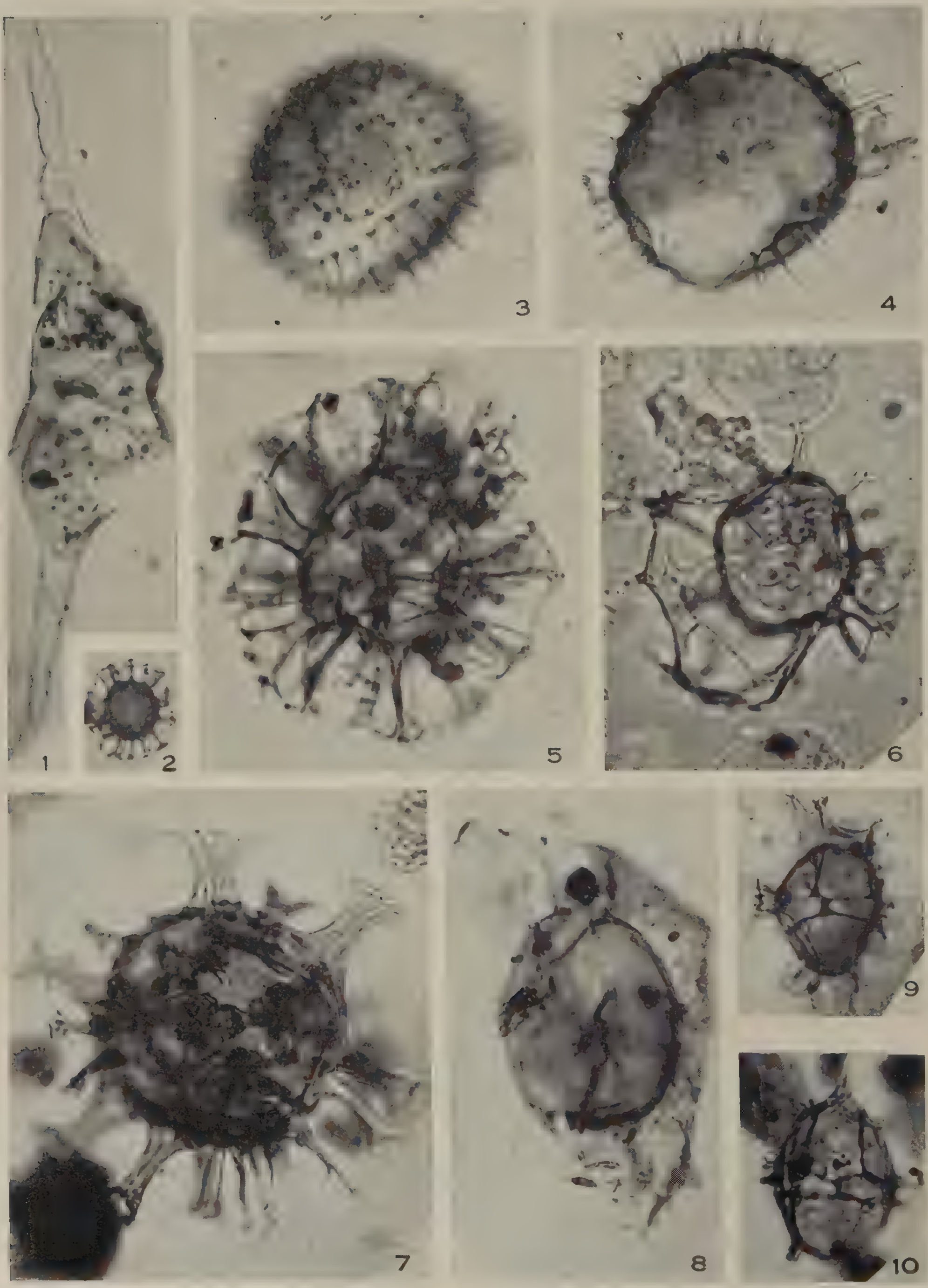
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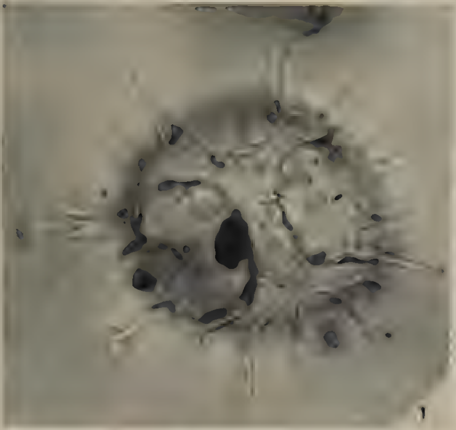
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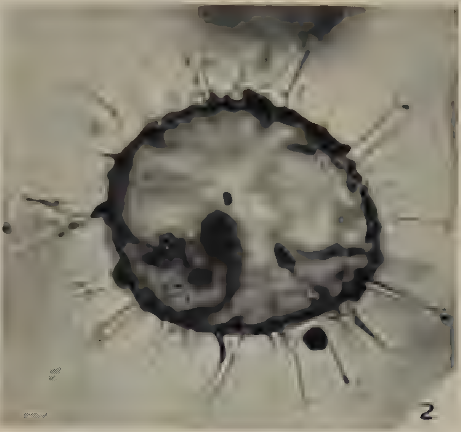
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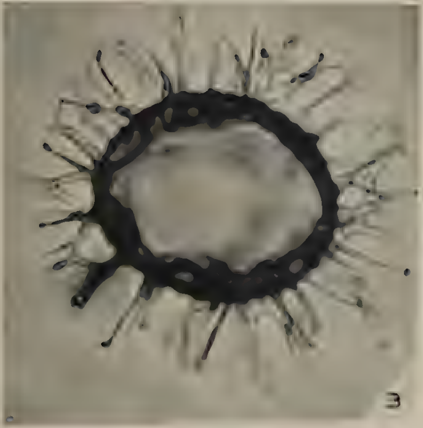
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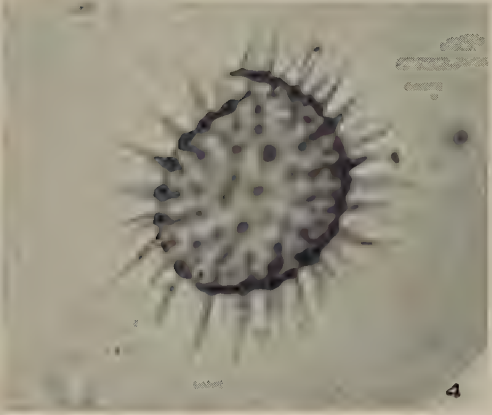
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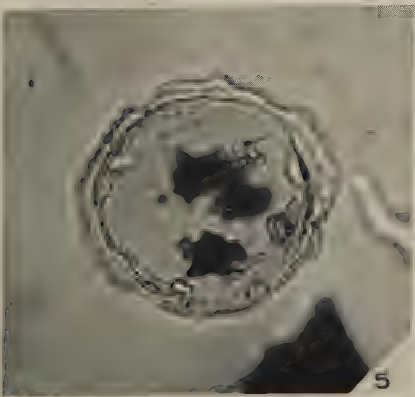
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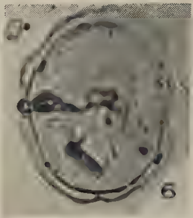
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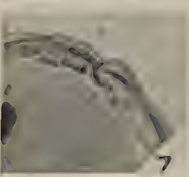
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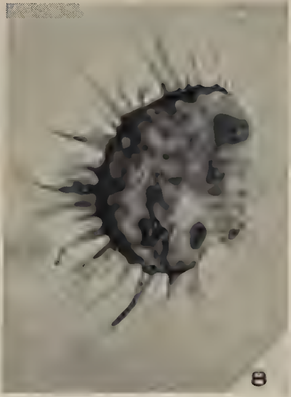
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PUBERTY, PHYSICAL MATURITY, AND RELATIVE GROWTH OF THE FEMALE HUMPBACK WHALE, *MEGAPTERA NODOSA* (BONNATERRE), ON THE WESTERN AUSTRALIAN COAST

By R. G. CHITTLEBOROUGH*

(*Manuscript received January* 24, 1955)

Summary

At puberty the mean body length of the female humpback whales on the Western Australian coast is 38.50 ± 0.18 ft. It is demonstrated that this length gives a reliable means of calculating the proportion of sexually immature females in a series where the lengths are known. Sexual maturity (based upon the first pregnancy) may either follow immediately upon puberty or be delayed for a further year. At the approach of physical maturity (when epiphysial fusion begins) the mean body length is 45.08 ± 0.29 ft. At this stage an average of 19 ovulations have occurred. On the available material, physical maturity is reached at a mean length of 44.34 ± 0.72 ft, when close to 30 ovulations have occurred. Growth in body length of sexually mature females becomes very slow even before epiphysial fusion begins. The significance of the high number of ovulations before the attainment of physical maturity is discussed. The proportion of physically mature individuals amongst the females in recent catches off the Western Australian coast is extremely low (1.8 per cent. of 457 females examined). The lengths of male and female humpback whales at puberty, at the approach of physical maturity, and at physical maturity are compared.

I. INTRODUCTION

In research upon whales, previous authors have referred to that period when reproductive activity first commences as the attainment of "sexual maturity". Matthews (1937) considered that "sexual maturity" was reached in female humpback whales from the South Atlantic region at a body length of 12.5 m (41 ft). In the northern hemisphere, Pike (1954) referred to "sexual maturity" as being reached in female humpback whales at approximately 40 ft, but gave no data to confirm this.

In male humpback whales as discussed in a previous paper (Chittleborough 1955), puberty (when reproduction first becomes possible) and sexual maturity (when full reproductive capacity has been attained) are distinct phases separated by an interval of at least 1 year. In the present paper, puberty and sexual maturity are distinguished in the female humpback whale also and the relationship between these two phases is discussed.

There are very few previous data upon physical maturity in female humpback whales. Matthews recorded relevant information concerning five females whose vertebral epiphyses were examined. One of these females was physically mature while another was approaching this condition. In the case of fin and blue whales, much more data upon body length

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and total "corpora lutea" has been accumulated (Wheeler 1930; Laurie 1937; Brinkmann 1948; Nishiwaki and Oye 1948).

The method of examining the vertebral epiphyses for physical maturity has been previously described (Chittleborough 1955). As for male humpback whales, those females in which epiphysial fusion had begun but not extended throughout the vertebral column were classed as approaching physical maturity, while those having all epiphyses fused to their respective vertebrae were physically mature.

This material was collected at Western Australian shore-based whaling stations from 1951 to 1954, and was supplemented by some ovaries preserved by inspectors of the Western Australian Fisheries Department during 1949 and 1950. In each year the observations were made between June and October, the period during which ovulation and parturition normally occurs (Chittleborough 1954).

II. Puberty

It has been shown (Chittleborough 1954) that in the ovaries of the larger immature female humpbacks the Graafian follicles are numerous and well developed, the largest having a mean diameter of 20 mm. During the first pro-oestrus one of these follicles further enlarges, exceeding 30 mm in diameter and protruding considerably from the ovarian surface (Chittleborough 1954, Plates 2 and 3) before rupture and the development of the first corpus luteum. From these characteristics it is a simple matter to distinguish female humpback whales as sexually immature, at puberty, or mature.

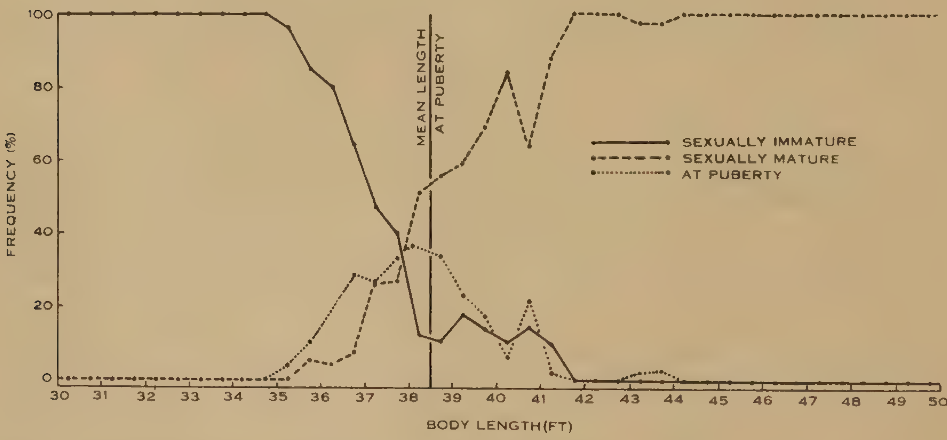

Fig. 1.—Proportions of sexually immature, pubertal, and mature females in 6-in. intervals of body length.

Of 821 females (from the Western Australian coast) whose ovaries were examined, 154 were found to be sexually immature, 77 were at puberty, and 590 were sexually mature. The distribution of these three phases within 6-in. intervals of body length are shown in Table 1 and

TABLE 1

PROPORTIONS OF FEMALE HUMPBACK WHALES SEXUALLY IMMATURE, AT PUBERTY, AND MATURE: WESTERN AUSTRALIAN COAST, 1951-1954

Body Length	Total Examined	Sexually Immature		At Puberty		Sexually Mature	
		No.	%	No.	%	No.	%
ft in. ft in.							
Under 34 0	11	11	100				
34 0 to 34 5	3	3	100				
34 6 to 34 11	11	11	100				
35 0 to 35 5	28	27	96.4	1	3.6		
35 6 to 35 11	20	17	85.0	2	10.0	1	5.0
36 0 to 36 5	25	20	80.0	4	16.0	1	4.0
36 6 to 36 11	14	9	64.3	4	28.6	1	7.1
37 0 to 37 5	34	16	47.1	9	26.5	9	26.4
37 6 to 37 11	15	6	40.0	5	33.3	4	26.7
38 0 to 38 5	41	5	12.2	15	36.6	21	51.2
38 6 to 38 11	28	3	10.7	10	35.7	15	53.6
39 0 to 39 5	39	7	17.9	9	23.1	23	59.0
39 6 to 39 11	36	5	13.9	6	16.7	25	69.4
40 0 to 40 5	49	5	10.2	3	6.1	41	83.7
40 6 to 40 11	28	4	14.3	6	21.4	18	64.3
41 0 to 41 5	52	5	9.6	1	1.9	46	88.5
41 6 to 41 11	32					32	100
42 0 to 42 5	50					50	100
42 6 to 42 11	34					34	100
43 0 to 43 5	46			1	2.2	45	97.8
43 6 to 43 11	41			1	2.4	40	97.6
44 0 to 44 5	41					41	100
44 6 to 44 11	22					22	100
45 0 to 45 5	38					38	100
45 6 to 45 11	21					21	100
46 0 to 46 5	19					19	100
46 6 to 46 11	15					15	100
47 0 to 47 5	9					9	100
47 6 to 47 11	5					5	100
48 0 to 48 5	7					7	100
48 6 to 48 11	1					1	100
49 0 to 49 5	3					3	100
49 6 to 49 11	1					1	100
50 0 to 50 5	1					1	100
50 6 to 50 11	0					0	—
51 0 to 51 5	0					0	—
51 6 to 51 11	1					1	100
Total	821	154		77		590	

Figure 1. The 77 females at puberty ranged from 35 ft 3 in. to 43 ft 6 in. in length, with an arithmetic mean length of 38.50 ± 0.18 ft. The median length (38.42 ft) of these females agreed closely with the mean length.

Hence the average length at which female humpback whales reach puberty on the Western Australian coast is 38 ft 6 in. This length, as discussed below, affords a reliable method of determining the proportion of sexually immature females in a sample where only the body lengths are available.

III. SEXUAL MATURITY

In defining sexual maturity as the attainment of full reproductive capacity, Asdell (1946) pointed out that in some mammals the female produces a smaller litter from the first pregnancy than from succeeding ones, so that sexual maturity does not necessarily coincide with puberty. Since single births are the rule in the humpback whale, the females of this species must be considered as sexually mature when the first pregnancy occurs.

Some female humpback whales become pregnant at the first ovulation, so that in these females sexual maturity follows immediately upon puberty.

However, conception often does not succeed during the first ovulatory season, as shown by a number of young females whose ovaries contained one (or sometimes two) corpora albicantia while the mammary glands had not yet been active, closely resembling the glands of immature females both in size and structure. Twenty-nine females were found to be in this condition. Their lengths ranged from 36 ft 6 in. to 42 ft 6 in. with a mean value of 39.66 ± 0.31 ft. These females would probably have become pregnant for the first time during their second ovulatory season, so that sexual maturity would be reached 1 year after puberty in such cases.

IV. PHYSICAL MATURITY

(a) *Physical Maturity and Body Length*

Table 2 shows the distribution of the body lengths of 457 female humpback whales whose epiphyses were examined, the whales being classified as physically immature, approaching physical maturity, or physically mature. There is a wide range of body length within which physical maturity may be reached, the shortest physically mature female being 41 ft 8 in. long, while the epiphyses of one 49 ft 3 in. long were still unfused and another female 51 ft 10 in. long was approaching physical maturity. The proportion of physically mature females in this series is surprisingly low; this aspect is discussed below.

Table 3 lists the body lengths of those females approaching and at physical maturity. The arithmetic mean length of the 46 females approaching physical maturity is 45.08 ± 0.28 ft, which is in close agreement with the median (lying between 44.92 and 45.00 ft). The mean length of the eight physically mature females is 44.34 ± 0.72 ft. It would be expected that the mean length at physical maturity would be slightly greater than that at the approach of physical maturity (this has been demonstrated for male humpbacks (Chittleborough 1955)). The mean length of females at physical maturity would probably be slightly higher if a larger number of specimens were available.

TABLE 2

EPIPHYSIAL FUSION IN FEMALE HUMPBACK WHALES: WESTERN AUSTRALIAN COAST, 1951-1954

Body Length	Number Examined	No Epiphysial Fusion		Fusion Begun		Full Fusion	
		No.	%	No.	%	No.	%
ft in. ft in.							
Under 34 0	6	6	100				
34 0 to 34 5	3	3	100				
34 6 to 34 11	6	6	100				
35 0 to 35 5	16	16	100				
35 6 to 35 11	11	11	100				
36 0 to 36 5	12	12	100				
36 6 to 36 11	7	7	100				
37 0 to 37 5	18	18	100				
37 6 to 37 11	8	8	100				
38 0 to 38 5	26	26	100				
38 6 to 38 11	17	17	100				
39 0 to 39 5	18	18	100				
39 6 to 39 11	24	24	100				
40 0 to 40 5	24	24	100				
40 6 to 40 11	22	22	100				
41 0 to 41 5	30	30	100				
41 6 to 41 11	19	18	97.7			1	5.3
42 0 to 42 5	26	23	88.5	3	11.5	0	
42 6 to 42 11	24	22	91.7	2	8.3	0	
43 0 to 43 5	26	20	77.0	4	15.4	2	7.6
43 6 to 43 11	25	22	88.0	3	12.0	0	
44 0 to 44 5	29	19	65.5	8	27.6	2	6.9
44 6 to 44 11	11	8	72.7	3	27.3	0	
45 0 to 45 5	14	6	42.9	7	50.0	1	7.1
45 6 to 45 11	10	4	40.0	5	50.0	1	10.0
46 0 to 46 5	7	5	71.4	2	28.6	0	
46 6 to 46 11	6	4	66.7	2	33.3	0	
47 0 to 47 5	4	3	75.0	1	25.0	0	
47 6 to 47 11	3	0	0	3	100	0	
48 0 to 48 5	2	0	0	1	50.0	1	50.0
48 6 to 48 11	0	—	—	—	—	—	—
49 0 to 49 5	2	1	50.0	1	50.0	0	
49 6 to 49 11	0	—	—	—	—	—	—
50 0 to 50 5	0	—	—	—	—	—	—
50 6 to 50 11	0	—	—	—	—	—	—
51 0 to 51 5	0	—	—	—	—	—	—
51 6 to 51 11	1	0	—	1	100	0	
Total	457	403	88.2	46	10.0	8	1.8

TABLE 3

FEMALES APPROACHING AND AT PHYSICAL MATURITY

Epiphysial Fusion Begun								Full Fusion	
Body Length (ft)	Total "Corpora Lutea"	Body Length (ft)	Total "Corpora Lutea"	Body Length (ft)	Total "Corpora Lutea"	Body Length (ft)	Total "Corpora Lutea"	Body Length (ft)	Total "Corpora Lutea"
42.00	17	44.00	12	45.00	23	46.25	19	41.67	31
42.33	19	44.17	29	45.08	24	46.50	23	43.00	29
42.42	21	44.25	18	45.25	15	46.92	24	43.00	36
42.67	12	44.25	18	45.33	17	47.08	19	44.00	35
42.83	20	44.25	24	45.33	31	47.67	21	44.00	37
43.00	12	44.33	18	45.42	18	47.75	11	45.25	27
43.08	—	44.33	24	45.50	11	47.75	22	45.50	33
43.17	17	44.33	32	45.50	25	48.25	25	48.33	38
43.42	16	44.83	14	45.50	30	49.25	22		
43.58	18	44.83	22	45.58	15	51.83	23		
43.58	28	44.92	11	45.58	31				
43.75	13	45.00	19	46.00	14				

(*b*) *Physical Maturity and Total "Corpora Lutea"*

The total "corpora lutea" in the ovaries refers to the number of ovulations which have occurred, irrespective of whether represented by newly formed corpora lutea, corpora graviditata, or corpora albicantia. As discussed by Mackintosh (1942), corpora albicantia persist in the ovaries of whales, so that the total "corpora lutea" may be used as an index of relative age.

In the 46 females which were approaching physical maturity (see Table 3), the total "corpora lutea" ranged from 11 to 32 with a median value of 19, which agrees closely with the mean (19.9). From this evidence, epiphysial fusion usually begins in female humpback whales when 19 ovulations have occurred.

Figure 2 shows the body length and total "corpora lutea" of 441 females examined by the author on the Western Australian coast, indicating those physically immature, approaching physical maturity, and physically mature. Of 36 females which had ovulated 19 or more times the epiphyses had not yet begun to fuse in only three (8.3 per cent.).

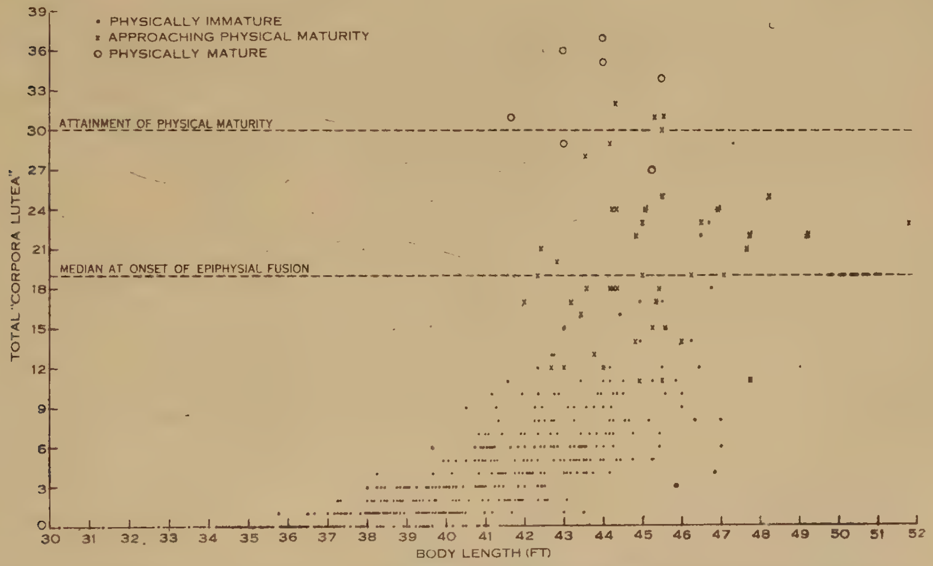

Fig. 2.—Total "corpora lutea" and physical condition (based on vertebral epiphyses) of female humpback whales taken off the western coast of Australia.

On the eight available records of physically mature females it is difficult to establish the number of "corpora lutea" which have accumulated when female humpback whales attain physical maturity. However, the distribution of the total "corpora lutea" of these eight individuals, together with those of the females approaching physical maturity (see Fig. 2), indicates that at physical maturity some 30 "corpora lutea" have accumulated in the ovaries of the female humpback whale.

V. Relative Growth Rate

It is now generally accepted (see Mackintosh 1942) that in whales the corpora albicantia persist, if not throughout life, then at least until well after physical maturity has been reached. Assuming that the ovulation rate remains relatively constant throughout life, the total "corpora lutea" in the ovaries may be used as an index of relative age in female whales.

Table 4

RELATIONSHIP BETWEEN BODY LENGTH AND RELATIVE AGE, USING NUMBERS OF OVULATIONS PRIOR TO SEASON OF KILLING AS INDEX OF RELATIVE AGE

Total Ovulations prior to Season of Killing	Number of Females	Body Length (ft)			
		Min.	Max.	Mean	Standard Deviation
0*	77	35.25	43.50	38.50	0.18
1	74	35.50	43.00	39.47	0.17
2	69	36.00	45.83	40.25	0.22
3	52	38.00	46.83	41.21	0.28
4	61	38.25	46.33	42.33	0.20
5	38	39.92	46.58	42.52	0.32
6	46	39.67	47.00	43.00	0.24
7	38	40.83	47.00	43.14	0.25
8	33	40.50	48.25	43.98	0.32
9	21	40.00	47.83	43.12	0.35
10	17	41.00	46.50	43.58	0.40
11	21	39.83	47.75	44.29	0.42
12-14	29	42.00	50.17	45.23	0.39
15-17	17	42.00	49.00	45.37	0.43
18-20	21	41.00	47.08	44.79	0.38
21-23	17	41.83	51.83	46.50	0.58
24-26	16	43.67	48.25	45.49	0.32
28-30	10	43.00	48.75	45.51	0.65
31-38	7	43.00	48.33	44.96	0.66

* At puberty.

On the Western Australian coast, female humpback whales are killed from June to October, the period during which oestrous cycles and parturition occur. This means that some females are taken shortly after ovulation (so that a newly formed corpus luteum is present), while others are killed during pro-oestrus. In order to apply a uniform standard of relative age, any ovulations which occurred just prior to killing must be omitted. Hence as an index of relative age the author has used the total number of ovulations which had occurred in seasons prior to that in which the whale was killed. These ovulations may be represented either by corpora albicantia alone, or in females in very advanced pregnancy would include the corpus graviditatum, as this would represent an ovulation in the previous season.

Table 4 shows the ranges and mean lengths of 587 sexually mature females, grouped according to the number of ovulations which had occurred prior to the season of killing, and also the range and mean length of 77 females killed at puberty (representing group 0, as these had not ovulated in previous seasons). The mean length of each group is shown against the number of previous ovulations in Figure 3.

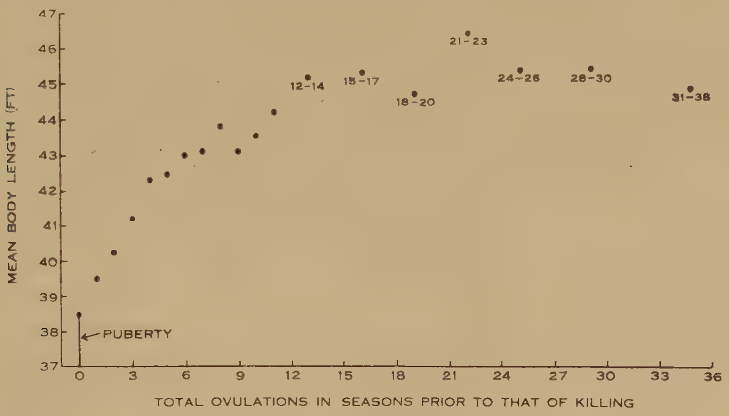

Fig. 3.—Growth curve for female humpback whales from the Western Australian coast, using as an index of relative age the total ovulations in seasons prior to that of killing.

Using the number of previous ovulations as an index of relative age, the mean lengths in Figure 3 indicate the growth curve of sexually mature female humpback whales in the stock fished off the Western Australian coast. The mean length is shown to increase with relative age at a decreasing rate until the curve approaches a horizontal line. This curve shows that growth in length has almost ceased long before physical maturity (based on full epiphysial fusion) has been reached (at approximately 30 ovulations). The apparent slight drop in the mean length of relatively old females (31-38 previous ovulations) is probably due to the small number of these females which were found, rather than to a real decrease in length as females aged.

No such relative growth curves are available for female humpback whales taken in other regions, but that given in Table 4 and Figure 3 might be used in a comparison of the growth of female humpback whales from different areas. Using this method, Pike (1953) has clearly demonstrated that the growth of female fin whales from the northern hemisphere is much slower than that of those from the southern hemisphere.

VI. Discussion

While the mean length of female humpback whales at puberty is 38 ft 6 in., the recorded range is very wide (35 ft 3 in. to 43 ft 6 in.). As previously discussed (Chittleborough 1954) this might be the result of some females reaching puberty when 2 years of age and others at 3 years.

The distribution of the body lengths of the 77 females at puberty has been analysed in this regard, but the data are incapable of supporting this hypothesis. It is still possible that puberty is not reached until the third year in some females, but the variable individual growth rates prevent this being demonstrated in the available material.

It was stated earlier that the mean length of female humpback whales at puberty (38 ft 6 in.) can be used to determine the proportion of sexually immature females in a sample where only the body lengths are known. As a test of the reliability of this method, the 821 females whose ovaries have already been examined may be used. It was found that 200 (24.4 per cent.) of these were under 38 ft 6 in. in length, in close agreement with 188 (22.9 per cent.) which had not yet ovulated.

Sexual maturity (based on the first pregnancy) may either follow immediately upon puberty, or be delayed for a further year, the females then having an average length of 39.66 ± 0.31 ft. Because these two classes of females exist, it is not possible to indicate a single mean length of female humpback whales on reaching sexual maturity.

The rate of growth, initially relatively rapid, has so declined before epiphysial fusion commences that there is no significant difference in length between those females approaching and those having attained physical maturity, while many females within the length ranges of these stages are still physically immature, as shown by Figure 2.

Ovulation, on the other hand, continues in these older females, presumably at a rate similar to that in younger females. No evidence of a climacteric has been found in physically mature female humpback whales taken on the Western Australian coast. In several cases the ovaries carried large thin-walled cysts (Chittleborough 1954), probably degenerate follicles, but normal follicles were also present and ovulation had recently occurred in three of these females.

At physical maturity in the female humpback whale the ovaries have accumulated some 30 "corpora lutea". This is surprisingly high when compared with the corresponding findings in fin and blue whales shown in Table 5.

Assuming that comparable techniques were used for the determination of total "corpora lutea", the greater accumulation of "corpora lutea" in physically mature humpback females might be interpreted as indicating a higher frequency of ovulation in this species than in fin and blue whales. But it has been shown (Chittleborough 1954), that the number of ovulations occurring in one ovulatory period (June to October) is probably a little lower in humpbacks than that estimated by Peters (1939) for one ovulatory period (in a 2-year breeding cycle) of fin and blue whales. In fin and blue whales there is a lactation anoestrus so that ovulation occurs every second year. If a post partum ovulation regularly occurred in female humpback whales, the rate of accumulation of corpora albicantia would be double that in fin and blue whales, thus accounting for the higher number of "corpora lutea" in physically mature humpback whales (approximately double that of physically mature fin and blue whales).

TABLE 5

TOTAL "CORPORA LUTEA" IN FIN AND BLUE WHALES AT PHYSICAL MATURITY

Author	Fin Whales	Blue Whales
Wheeler (1930)	15	—
Laurie (1937)	—	11
Peters (1939)	14-15	12
Nishiwaki and Oye (1948)	14	12
Brinkmann (1948)	13	11-12

Although very convenient, there is not a great deal of evidence to support this hypothesis. A lactating female humpback suckling a very young calf (both taken recently by special permission for research purposes) was found to have ovulated shortly after parturition, and two other females were found to be in advanced pregnancy and yet in late stages of lactation. Hence post partum oestrus can occur in female humpback whales, but at present there is little indication that it is a regular feature in this species. The remaining conclusion accounting for the high number of "corpora lutea" in the ovaries of physically mature female humpback whales is that physical maturity is attained relatively later in the life of humpback whales than in fin and blue whales.

When taking whales the gunners select the larger individuals, yet in the representative series examined for physical maturity (Table 2), only 1.8 per cent. (eight in a total of 457) of the females had reached physical maturity. The proportion of physically mature males was similarly low, viz. 1.4 per cent. of 567 examined (Chittleborough 1955). Wheeler (1930) suggested that the proportions of physically mature whales might be a very useful index of the condition of the stock. However, in the humpback whale comparable records from past whaling ventures on the Western Australian stock are not available. Brinkmann (1948) found that 37.4 per cent. of 561 female fin whales and 22.4 per cent. of 295 female blue whales, taken in Antarctic areas II to IV in 1939-40, were physically mature. Similar proportions of physically mature female fin and blue whales have been reported by Wheeler (1930) and Laurie (1937).

As suggested for male humpback whales (Chittleborough 1955), the very low proportions of physically mature individuals in recent catches from the Western Australian coast might be due to:

(i) a migratory difference—physically mature individuals moving further offshore or not all leaving the Antarctic each autumn;

(ii) a species difference—epiphysial fusion occurring in humpback whales later in life than in other species of whales;

(iii) a fishing effect—previous heavy fishing with a strong selectivity towards larger individuals resulting in the removal of many physically mature individuals from the stock.

There is no evidence that the first possibility applies in this species but the much lower proportion of physically mature individuals in this than in other species of whales might be due in part to the already suggested later age at which humpback whales reach physical maturity. The very low percentages of physically mature humpback whales in recent catches off this coast might also be the result of previous heavy fishing upon this stock. Evidence of such changes within this stock is accumulating and will be considered in a later paper.

From the results of the investigation on the Western Australian coast, the lengths of male and female humpback whales from this stock can be compared at puberty and at the approach and attainment of physical maturity. These lengths are summarized in Table 6.

TABLE 6

LENGTHS OF MALE AND FEMALE HUMPBACK WHALES AT PUBERTY AND PHYSICAL MATURITY

Condition	Minimum	Maximum	Mean (ft)
	ft in.	ft in.	
Puberty:			
Males	33 4	40 10	36.75
Females	35 3	43 6	38.50 ± 0.18
Approaching physical maturity:			
Males	38 10	45 10	41.90 ± 0.17
Females	42 0	51 10	45.08 ± 0.29
Physical maturity:			
Males	39 10	45 6	42.97 ± 0.67
Females	41 8	48 4	44.34 ± 0.72

At all three phases the minimum, maximum, and mean body lengths of the females are greater than those of the males. The mean length of the females approaching physical maturity is significantly higher than that of the males at this stage ($t = 10.11$ on 124 degrees of freedom). The test of significance upon the females and males which had reached physical maturity was inconclusive ($t = 1.39$ on 14 degrees of freedom), no doubt owing to the small number of records of this stage at present available. It has long been known that female humpback whales grow faster, attaining greater lengths than the males, but the values in Table 6 indicate the degree to which this occurs.

VII. ACKNOWLEDGMENTS

The cooperation of the Norwest Whaling Company and the Australian Whaling Commission, enabling material to be collected from their respective stations at Point Cloates and Carnarvon, is gratefully acknowledged.

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THE MOVEMENTS AND MIGRATIONS OF MULLET (*MUGIL CEPHALUS* L.)

By J. M. THOMSON*

(*Manuscript received December* 3, 1954)

Summary

The mullet school (*Mugil cephalus* L.) has a real entity. The same fish remain associated in a group for a considerable period. Some emigration from (and inferentially immigration to) the school takes place. Some schools remain in one locality (within a river system) for some months. Others appear to move more or less continually. A sojourn in fresh water does not appear to be essential though many fish are found there. It is impossible to generalize about age preferences for salinity. Fish of all age groups can be found at all times of year from fresh water to the lower saline estuaries.

Some seasonal difference in the direction of movement is evident in Moreton Bay, Qld.; but this movement lacks the persistence of the seaward spawning migration of adult fish in late summer and autumn. There is some evidence to support the hypothesis that the majority of mature fish do not migrate every spawning season, but at greater intervals.

I. INTRODUCTION

Studies of the migrations of Australian sea mullet *Mugil cephalus* Linnaeus by Kesteven (1942, 1953) and Thomson (1951) have been concerned primarily with establishing the fact that the spawning migration is in a northerly direction. While making some new observations on the factors concerned with this migration, the present study is concerned more with the pattern of movement of the mullet within the river systems.

II. TAGGING OPERATIONS

Movements have been traced by tagging with a standard opercular tag (Kesteven 1942, 1953; Thomson 1951). This is suitable for sea mullet from approximately 10 cm L.C.F. (length to caudal fork) upwards. Table 1 shows the number of sea mullet tagged and the number and proportion of returns for each area.

Some of the data on tagging returns used here have already been published by Thomson (1951, Appendix III) and by Kesteven (1953, Appendix I). A further 265 tagging returns have been made. Details of these are on file at the Division of Fisheries, C.S.I.R.O., Cronulla, N.S.W.

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The conclusions embodied in this paper are based on these three sets of data.

TABLE 1

MULLET TAGGING STATISTICS

Location	Number Tagged	Tags Recovered	
		Number	Percentage
Western Australia			
Minor waters	2,531	18	0.71
Swan River	954	10	1.04
Leschenault Inlet	3,668	143	3.89
Peel Inlet	2,868	69	2.4
Total	10,021	240	2.39
Queensland			
Moreton Bay	2,425	98	4.04
Outside Moreton Bay	1,227	32	2.61
Total	3,652	130	3.56
New South Wales			
Pre-1946	3,435	224	6.52
Post-1946	380	12	3.16
Total	3,815	236	6.18

III. DISPERSAL OF POSTLARVAE AND FRY

The exact places of spawning have not been determined, but Kesteven (1942) expressed the opinion that they must be somewhere at sea, which is a logical deduction from the known facts of the movement of mature fish. This conclusion is supported by the fact that small mullet first become evident in the lowermost part of the estuaries. On such occasions the weather is calm and sunny. The tiny fry progress in an almost unbroken stream a few feet wide in shallow water along the shore.

No satisfactory method of marking such small fish has been achieved; consequently information on the movements of the fry is based solely on field observation. During 1951 observations on small mullet were made along a chain of stations from salt to fresh water in Moreton Bay (Qld.) and the inflowing Logan River with its principal tributary the Albert River (Fig. 4). After entry to the bay proper through the South Passage, the almost continuous band of fry disperses into small schools of some few hundred individuals. Whether some of these schools disperse directly across the bay through deep water is unknown. Certainly at first they are observable only in the shallows along Stradbroke and Moreton Islands. In early September the mullet fry were observed only on the flats between Amity Point and Dunwich (stations 1 and 2, Fig. 4). Later that month they were among the islands between Dunwich and the mouth of the Logan River, roughly as far as station 4. In mid October they were in the Logan

River at least as far as station 6 and in mid November were in the fresh water at the head of the tidal zone in the Albert River (station 7*a*).

Although some mullet fry reach the fresh water within 3 months of entering the bay, this does not imply that all the fry make their way there. Schools remain scattered along the whole length of the line from bay mouth to the fresh water. Lowered salinities certainly seem to attract the fry, as every creek along Stradbroke Island and the mainland is a centre of concentration, the shallows remote from a creek mouth rarely being occupied by mullet of the 0+ group.

IV. Movements of 0 Group Mullet

The 0+ age-group mullet are too small to tag successfully until they reach 10 cm L.C.F., by which time they are 10 or 11 months old. When the tide is in the small mullet can be observed scattering over the mud flats to feed. How far they move has been impossible to determine but generally it does not appear to be very far. Movement is continually taking place, for creeks netted out with fine mosquito netting become populated again in the course of 2 or 3 weeks.

In the freshwater zone of the Albert River the small mullet, 4-6 cm (size determined by seining), were observed to be most active (moving in the shallows and jumping) late in the afternoon till well after dark and again in the morning for an hour or two before and after dawn. Mullet of this size had no difficulty in mounting swiftly flowing rapids of up to 50 yards in length. By the time the mullet are 6-8 cm L.C.F. they are moving far afield over the flats, often in company with larger mullet with whom they may be taken in small-mesh seines such as garfish nets. Mullet of this size still enter the small creeks but apparently not in such great numbers as when smaller. Numbers of them can be seen well away from the creeks at all stages of the tide. No 0+ mullet have been reported from the sea beaches, nor do observations suggest that there is any movement of this class of fish towards the sea.

V. Movements of Immature Mullet

(*a*) *Group* I *Mullet*

Mullet of the I+ and older groups are large enough to tag with the standard operculum tag. Table 2 records the data on the age at tagging in relation to the age at subsequent recapture, with the proportion in each age group which was retaken in the river system where tagging took place or which had travelled to other water systems.

In determining the age classes at time of recapture an arbitrary birthday has been set at July 1. The majority of fish have spawned by then except in the north of Queensland.

I+ mullet are not generally believed to move from their home waters, but of the 137 mullet tagged and recaptured as I+ fish in Western Australia two had moved outside the estuary of origin. One of these was retaken on a sea beach only just outside Peel Inlet where it was tagged; the other, tagged in Leschenault Inlet, was retaken in the Swan River to the north only 60 days after tagging. Nevertheless the evidence is that the majority of I+ mullet remain in the one river system, within which there

TABLE 2

AGE AT TAGGING AND AT RECAPTURE

Discrepancy in the totals between Table 2 and Table 1 is due to lack of information on some fish

Age		Location of Recapture		
When Tagged	When Retaken	State	Same River	Travelled
I+	I+	W.A.	135	2
		Qld.	3	
		N.S.W.	3	
	II+	W.A.	35	4
		Qld.	3	
		N.S.W.	15	4
	III+	W.A.	1	
		N.S.W.	2	4
	IV+	W.A.	2	
		N.S.W.		1
	VI+	W.A.	1	
II+	II+	W.A.	40	5
		Qld.	43	
		N.S.W.	69	2
	III+	W.A.	1	
		Qld.	25	2
		N.S.W.	37	39
	IV+	Qld.	1	
		N.S.W.	4	4
III+	III+	W.A.	1	1
		Qld.	23	3
		N.S.W.	90	1
	IV+	Qld.	4	2
		N.S.W.	16	2
	V+	N.S.W.		1
IV+	IV+	Qld.	1	
		N.S.W.	7	2
	V+	Qld.	1	
		N.S.W.	3	7
V+	V+	N.S.W.	4	1
VII+	VII+	N.S.W.	1	

may be considerable movement without any obvious pattern of movement when analysed in terms of time of tagging or time of recapture (Fig. 1).

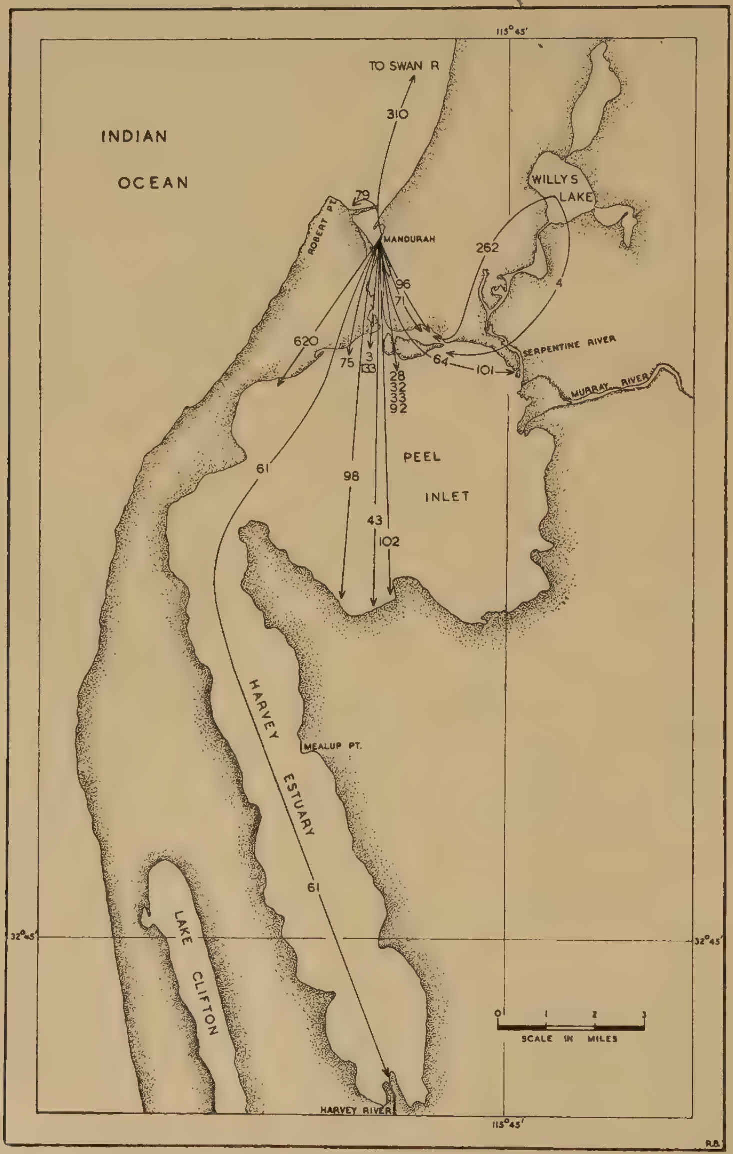
115°45'
TO SWAN R
310
INDIAN
OCEAN
79
ROBERT PT.
MANDURAH
WILLYS
LAKE
262
4
96
71
620
75
3
133
64
101
SERPENTINE RIVER
28
32
33
92
MURRAY RIVER
PEEL
INLET
61
98
43
102
HARVEY
ESTUARY
MEALUP PT.
61
LAKE
CLIFTON
32°45'
32°45'
0
1
2
3
SCALE IN MILES
HARVEY RIVER
115°45'
R.B.

Fig. 1.—Movements of I+ mullet in Peel Inlet, W.A. Numbers indicate the days of freedom between tagging and recapture.

The early returns come from close to the tagging place, as is to be expected; but some fish were recaptured close by after several weeks at liberty, suggesting either that movement of the school is slow or else that the school tends to forgather repeatedly in the one area.

(*b*) *Group* II *Mullet*

These are the fish which participate in the "hard-gut" migration in early summer (Kesteven 1942, 1953; see also Fig. 2). This run of fish does not take place invariably, as the hard-gut run fails to appear in some years. The possible stimulus to the movement is discussed in Section IX. The data (Table 2) suggest that between 4 and 5 per cent. of the population in a particular river may take part in this type of movement. The eight fish recorded as having been tagged as I+ fish and recaptured as II+ fish may have moved as I+ fish and failed to be recaptured until they became II+ fish, but even if these be ignored the percentage of travelled fish remains the same.

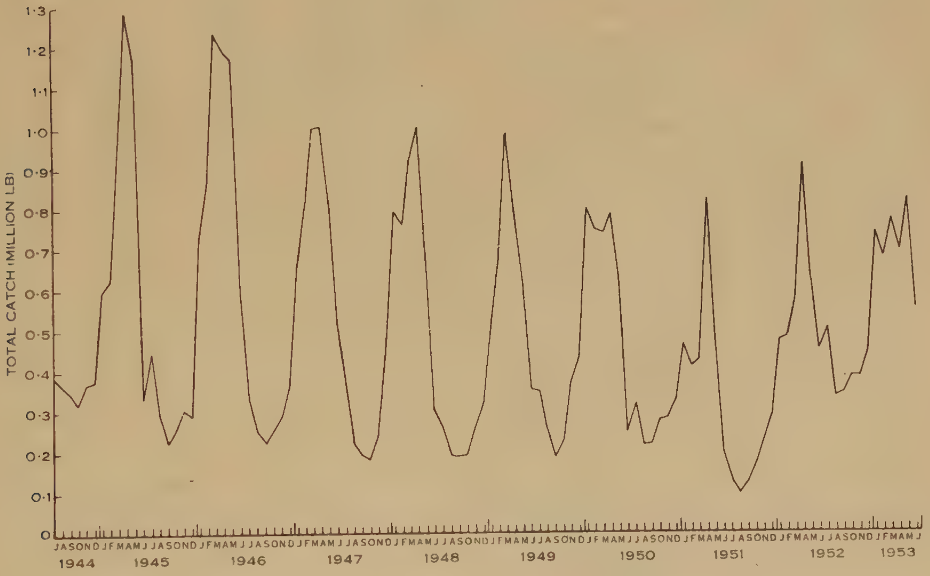

Fig. 2.—Monthly mullet catch, New South Wales, 1944-1953.

Within the estuaries, however, there is a considerable movement of II+ mullet, yet some of these have been returned after long intervals from the tagging spot. It is possible that such fish had wandered far before returning to their earlier haunts but this does not seem feasible.

In Peel Inlet, W.A. (Fig. 3) there is an indication that mullet entering from the Serpentine River first visit the southern estuary (50-117 days) and then move to the channel leading out to sea (96-161 days), but there were two fish of the same size group and age group which had left the estuary and had been recaptured in the Swan River only 50 days after tagging. Differences in time of tagging do not apply, as all the fish were tagged in July 1952 or July 1953.

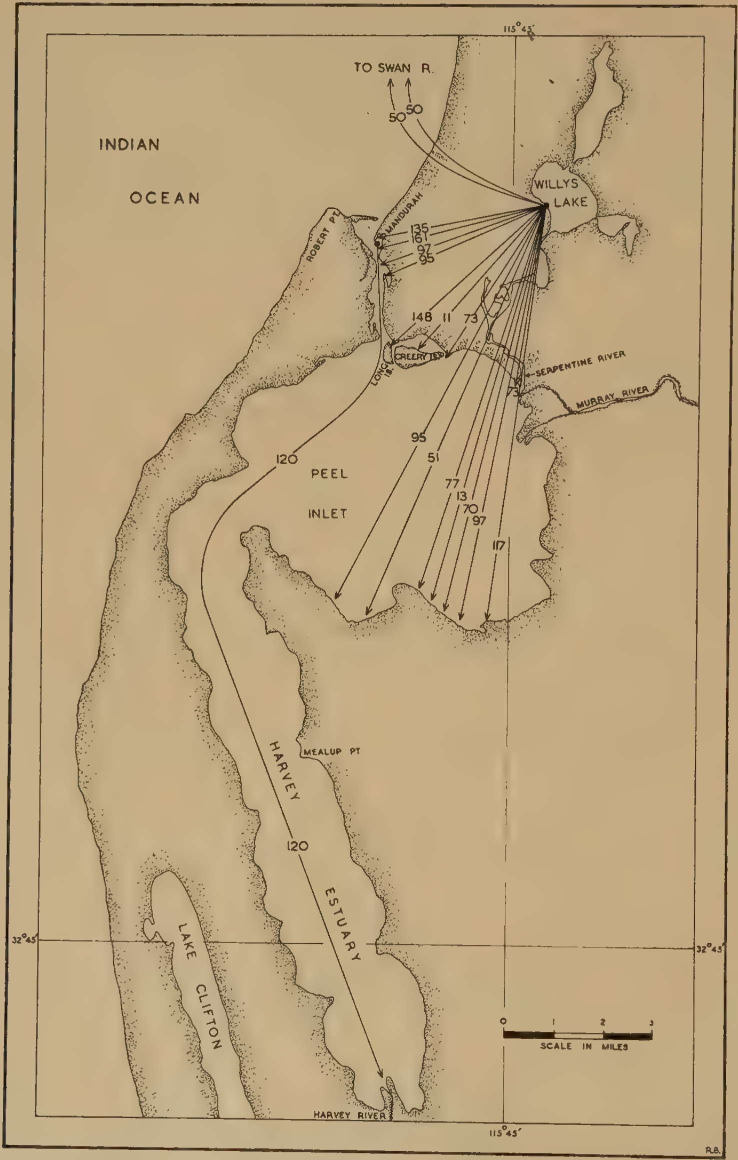
115°45'
TO SWAN R.
50
50
INDIAN
OCEAN
WILLYS
LAKE
ROBERT PT
MANDURAH
135
161
97
95
148
11
73
CREERY IS
LONG IS.
SERPENTINE RIVER
MURRAY RIVER
73
95
51
120
PEEL
INLET
77
13
70
97
117
HARVEY
MEALUP PT
120
ESTUARY
LAKE
CLIFTON
32°45'
32°45'
0
1
2
3
SCALE IN MILES
HARVEY RIVER
115°45'
R.B.

Fig. 3.—Movements of II+ mullet in Peel Inlet, W.A. Numbers indicate the days of freedom between tagging and recapture.

In Moreton Bay, Qld., there also seems to be a seasonal difference in the movements (Fig. 4). In summer the movements in the bay are southward until some time in April or occasionally May; but from April until June most returns have been from points north of the tagging spot. This northward movement may be considered as the early part of the spawning migration in which mullet first participate at the end of the II+ year.

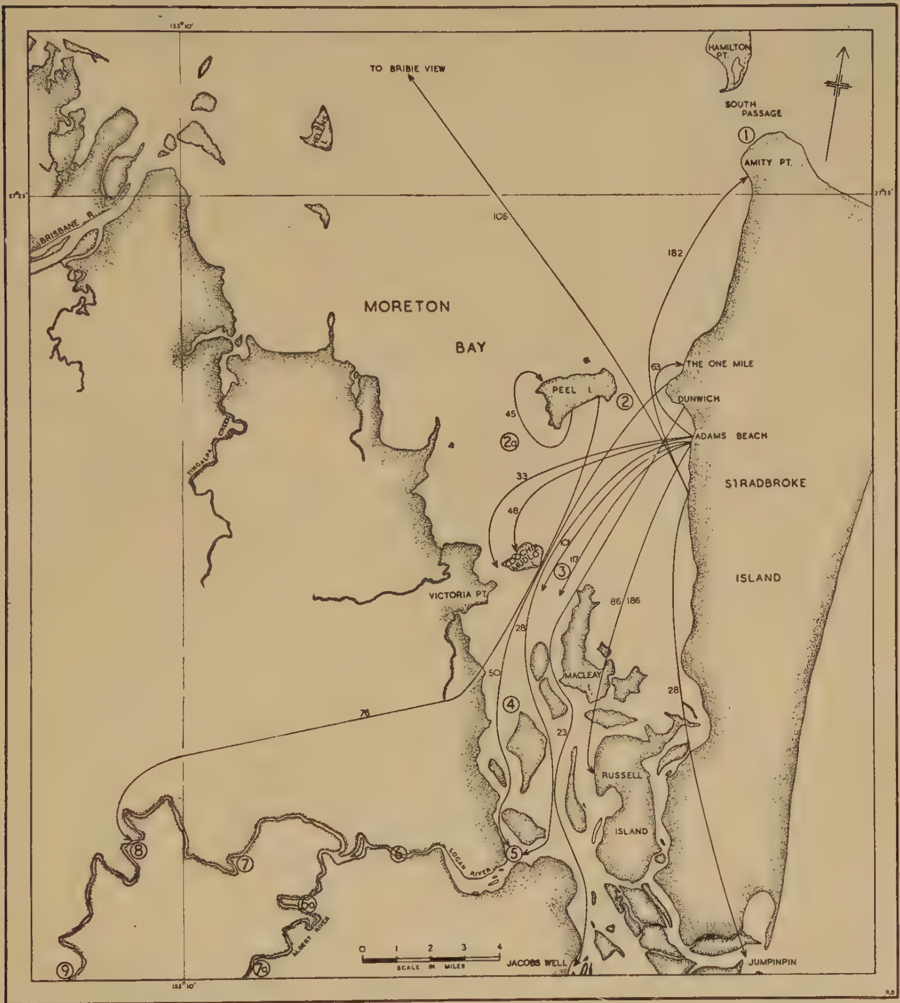
153°10'
TO BRIBIE VIEW
HAMILTON PT.
SOUTH PASSAGE
①
AMITY PT.
27°25'
BRISBANE R.
106
182
MORETON
BAY
63
THE ONE MILE
PEEL I.
②
DUNWICH
45
②a
ADAMS BEACH
STRADBROKE
33
48
ISLAND
③
17
VICTORIA PT.
86/186
28
50
MACLEAY I.
28
④
76
23
RUSSELL
ISLAND
⑧
⑦
⑥
⑤
LOGAN RIVER
⑥a
ALBERT RIVER
⑦a
⑨
0 1 2 3 4
SCALE IN MILES
JACOBS WELL
JUMPINPIN

Fig. 4.—Movements of II+ mullet tagged in Moreton Bay, Qld., and retaken as II+ fish. Numbers circled are station figures referred to in the text. Other numbers are the days of freedom.

VI. Mature Mullet

As early III+ fish the mullet are taking part in and returning from the spawning run (at least in Queensland waters; the run is earlier in summer in New South Wales). The movements of mullet tagged as II+ Those tagged in December before the commencement of the spawning fish in Moreton Bay and recaptured as III+ fish are shown in Figure 5. migration were all taken within the bay at places south of the tagging spot, but after such long periods that they could have moved to sea on their spawning migration and returned to the bay. Those tagged during the height of the spawning migration were returned from July to November north of the tagging spot, two even passing to other river systems, but from November onwards a residual southerly movement was apparent, suggesting that these fish may have returned to the bay and moved south after the spawning migration.

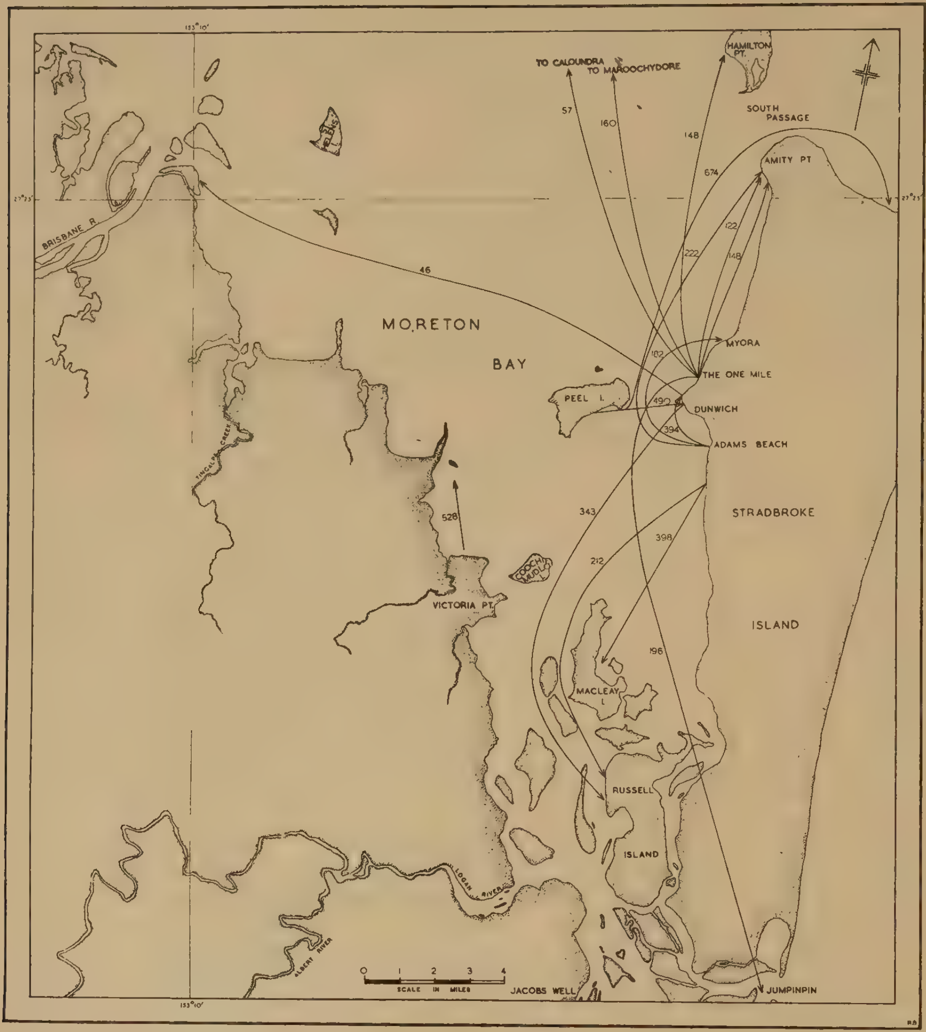
153°10'
TO CALOUNDRA
TO MAROOCHYDORE
HAMILTON PT.
SOUTH PASSAGE
57
160
148
674
AMITY PT
27°25'
BRISBANE R.
122
222
148
46
MORETON
BAY
MYORA
102
THE ONE MILE
PEEL I.
490
DUNWICH
394
ADAMS BEACH
STRADBROKE
ISLAND
343
398
212
528
VICTORIA PT.
COOCHIE MUDLO
196
MACLEAY I.
RUSSELL
ISLAND
TINGALPA CREEK
LOGAN RIVER
ALBERT RIVER
0 1 2 3 4
SCALE IN MILES
JACOBS WELL
JUMPINPIN
RB

Fig. 5.—Movements of II+ mullet tagged in Moreton Bay, Qld., and retaken as III+ fish. Numbers are the days of freedom.

There is some evidence that if feeding is disrupted during the months prior to the spawning migration some fish of mature age do not produce ripe gonads and do not take place in the spawning run (Thomson 1953*b*), but the majority of III+ mullet may be presumed to have taken part in one spawning run. The number of cases listed in Table 2 is not very great but they support the contention of Kesteven (1953, hypothesis 4, p. 273) that a particular fish may not migrate every year after first maturing. From the tagging returns it would appear that more fish migrate at the end of their II+ and IV+ years than at the end of the III+ year. On the other hand some fish tagged as I+ fish have been retaken as IV+ and even VI+ fish, still in the same river system in which they were tagged. It is impossible to determine whether these had in fact moved to sea, spawned, and returned.

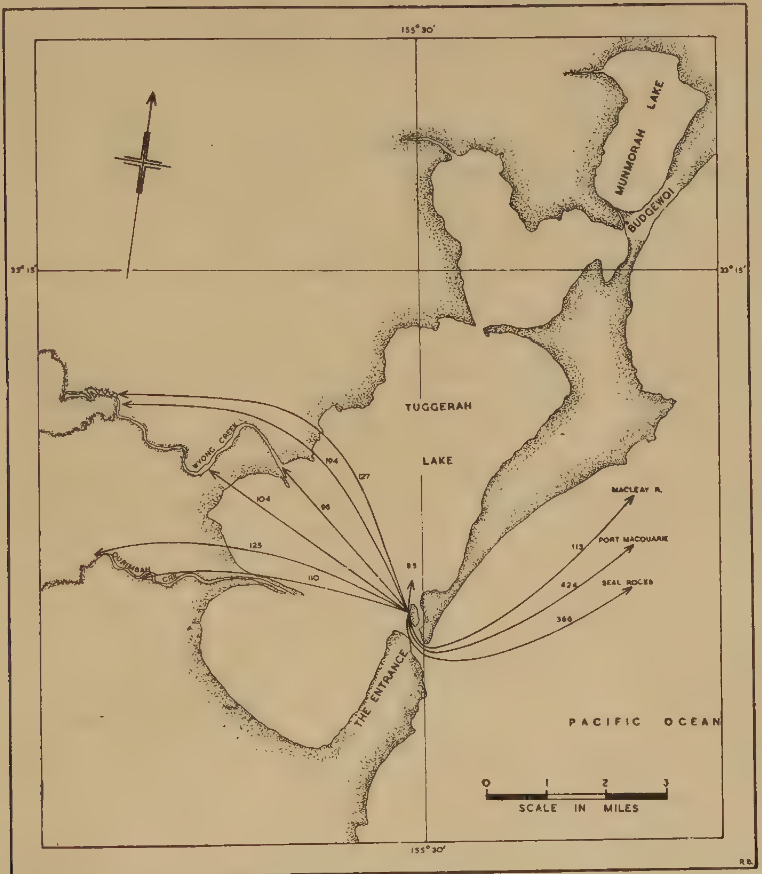
155° 30′
MUNMORAH LAKE
BUDGEWOI
33° 15′
33° 15′
TUGGERAH
LAKE
WYONG CREEK
OURIMBAH CR
194
127
104
96
125
110
85
MACLEAY R.
113
PORT MACQUARIE
424
SEAL ROCKS
366
THE ENTRANCE
PACIFIC OCEAN
0
1
2
3
SCALE IN MILES
155° 30′
R.B.

Fig. 6.—Movements of III+ mullet tagged in Tuggerah Lakes, N.S.W., on a single occasion. Numbers are the days of freedom.

Insufficient III+ or older fish were tagged and recovered in any one locality to give a picture of local movements except at Tuggerah Lakes, N.S.W. (Fig. 6). The first fish to be recovered was taken 85 days later only 500 yards from the tagging spot. The next two came from Wyong

Creek. Two later returns also came from Wyong Creek but meanwhile one had been retaken in Ourimbah Creek. Before this, however, one fish had been retaken in the Macleay River some distance to the north of Tuggerah Lakes. The last two returns from this tagging operation were also from travelled fish, one being taken at Myall Lakes, the other at Port Macquarie, 70 and 160 miles to the north respectively.

VII. Schooling

Breder and Halpern (1946) define a fish school as being an aggregation where "all individuals are similarly oriented, uniformly spaced and moving at a uniform pace". This state of affairs is obviously transitory. Any fish school maintained under observation changes its outline frequently. The aquarium tank is an unnatural environment but small fish do school in them. The author has observed schools of 30 or so II+ mullet and separate groups of a few older fish in aquaria at Trivandrum, India, and at Arcachon in France. The small fish keep approximately equal distances from those beside them, but the distances from fish in front, behind, above, and below constantly varies. The position of a particular fish in such a school is not constant; some alteration in the position of each fish is constantly occurring.

When the fish reach the end of the tank the leaders turn but the whole school does not turn with them as demanded by the definition of Breder and Halpern. The leaders pass back through the advancing school, whose members turn one by one as they reach the tank wall. Occasionally a fish will turn before reaching the wall, especially if its passage is blocked by a fish turning in front of it.

Observations of mullet schools on the shallow mud flats at Stradbroke Island, Moreton Bay, suggest that this picture may reflect what happens in nature. The shape of a mullet school is continually changing. It may change rapidly from a compact oval mass to a long narrow band. Group reaction occurs in the school. A swerve by the leaders is faithfully followed by those behind, but not infrequently a movement may be initiated by fish from the body of the school moving in a new direction. The school seems as likely to follow such new initiative as the original leadership. Often when such a movement occurs the school may split into two for a short while, some fish following each leading group. Usually the two groups come together again quickly. The leadership does not seem to be permanent. Besides the frequent new directive initiative displayed by members of the school, those in front are often passed by others who temporarily lead the way.

VIII. Permanence of the Schools

Kesteven (1946, 1947) has described the mullet as being scattered in fresh water during the non-migration season. This may be so with older (say III+ or more) fish. On 12 occasions nets were set and hauled by the author in the upper Albert River where the salinity is less than 1‰ (Rochford 1953*a*, 1953*b*). On all 12 occasions some specimens of *M. cephalus* were taken, but on four of these the only ones taken were 0+ fish, too small to carry a tag. On the other eight occasions a total of 237 mullet were taken; on four occasions they were taken in sufficient quantity for it to be assumed that the mullet were schooled (the numbers taken being 81, 56, 36, and 36). Only a few fish were taken on the other occasions (13, 7, 6, and 2). Very few really large mullet were taken (Table 3).

TABLE 3

SIZE FREQUENCIES OF MULLET TAKEN IN FRESH WATER, ALBERT RIVER

Size Group (cm)	5-9.9	10-14.9	15-19.9	20-24.9	25-29.9	30-34.9	35-39.9	40-44.9
Number	3	73	53	9	45	51	2	1

Of the 51 in the 30-35 cm group, 46 were taken at one time, in August. Older age groups are represented in the commercial fish catch to any extent only in the months of March, April, and May (Kesteven 1942, Table 5). The suggestion by Kesteven is that during the remainder of the year the fish are scattered in the fresh water. In Western Australia the fresh waters are very restricted in extent and indeed most of them dry up to a series of unconnected pools during the summer months. Instead there appears to be a concentration of older fish in Shark Bay and the Abrolhos Islands, where it would appear that a permanently marine habitat has been adopted (Thomson 1950, 1953*a*). There they are schooled and taken throughout the year (Thomson 1950). Saville-Kent (1893) records finding this species amongst coral islets on the Barrier Reef north of Cooktown, Qld. Professor W. Stephenson of the University of Queensland is at present carrying out observations at Heron Island, on the Barrier Reef, which should determine whether permanent marine concentrations corresponding to the Shark Bay schools of sea mullet exist also on the east coast of Australia.

As applied to fish in the lower estuary the term scattered can be used only in a relative sense. The fish are still schooled up but in much smaller schools than appear during the spawning migration.

The entrance of juvenile 0+ fish to a river system is achieved by a more or less continuous band of fry which may not merit the term school. This band breaks up into small schools as it spreads over the estuary.

From direct observation of mullet of all sizes feeding on the sand and mud flats it can be said that at least during daylight hours, the fish spread over the flat singly or in small groups while feeding. When moving in response to some stimulus or when disturbed the fish school up and swim away. At night fish seem to jump in a random scattered fashion suggesting that then, too, the fish are scattered. Norman (1931) quotes Boulenger as having observed young mullet to swim in a massed shoal in daylight, breaking up at night to scatter over the flat to feed. He states that if the fish are disturbed they come to the surface and re-form the school.

The evidence from tagging fish taken in a single haul of the net suggests that the schools have a permanence of at least 6 months or so, but some emigration from and presumably immigration to the schools occur. The apparent emigration may be due to a failure to rejoin the main school at the time of release from the tagging experiment. Similar confusion probably occurs when a school breaks up during commercial netting.

Sometimes two or more fish may be taken together weeks or months later, or fish will be returned one by one from near the spot where tagging took place. Yet besides these others may turn up elsewhere. For instance, a tagging experiment at Peel Island in Moreton Bay on December 10, 1951, gave some interesting results. A total of 158 II+ mullet were tagged prior to the travelling season. The returns show that two fish were retaken on the same ground where they were tagged, only 2 days after tagging. Others were taken from the same area 71, 95, 138, 175, and 215 days after tagging. Meanwhile one fish had been retaken 76 days after tagging in the fresh water of the upper Logan River. It is possible that the whole school swam up the river during these 5 days and then returned to Peel Island in the following 24; but in view of the behaviour of other schools, a more convincing hypothesis is that the main school remained in the same spot, while some fish left it, it being impossible to tell whether as a result of the tagging operation or of some subsequent stimulus.

It is interesting to note too from this same tagging that although one fish had travelled after 184 days to another water system (Maroochydore) a later tag was retaken after 490 days only 3 miles from the tagging place.

Several minor tagging experiments suggest this breaking up of schools. For instance, of the two mullet recorded in Table 2 as having been tagged as III+ fish in Western Australia one was retaken on a sea beach some miles to the north of Peel Inlet where it was tagged. A day later the other which had been tagged on the same occasion was retaken still inside the inlet. The school from Tuggerah Lakes described in Section V(*c*) also displayed a prolonged association of some individuals but in addition an indication of some fragmentation of the school.

In another experiment on March 7, 1952, 132 mullet were tagged at Adam's beach south of Dunwich, Qld. Eight tags were later returned. The first five retaken were close to the original tagging area. The sixth was retaken on the north side of Coochiemudlo Island some miles across the bay 48 days later, but 63 days after tagging another fish was taken in the opposite direction.

On another occasion (January 31, 1952) 56 mullet were tagged at Adam's Bay, Qld. Four were retaken. One fish was taken at Russell Island 86 days later. Two more were taken at Middle Bank, Redland Bay, one after 101 and the other after 117 days, suggesting that the school had remained for some days in the vicinity of Middle Bank, possibly proceeding there by way of Russell Island. The fourth fish was taken much later (222 days) to the north at Amity Point, possibly on its spawning migration.

Kesteven (1953) reports a group of 19 tagged mullet retaken in a haul in Port Hacking, N.S.W., on May 28, 1943, where they had earlier been tagged in four separate tagging experiments at three localities (his returns Nos. 135-152 and 154), suggesting that several small schools had united to move to sea or that the tagging hauls had fragmented a larger school on several occasions.

Another 14 fish from these same four experiments were recaptured at the same place on September 14, 1943 (Kesteven's returns Nos. 160-173), as were another take of 12 (his returns Nos. 179-190) on October 11, 1943.

In another case listed by Kesteven (his returns Nos. 21-53) 31 fish tagged in Port Hacking on May 13, 1940, were retaken together 125 days later in the Hawkesbury River, 40 miles to the north. With them were also taken two fish tagged in Port Hacking on November 3, 1939.

Thus it appears that mullet schools do retain their identity over long periods despite the scattering during feeding periods. They may also remain about one spot for considerable periods, but in other instances considerable wandering takes place.

IX. STIMULI

(*a*) *Non-spawning Movements*

Presumably most of the movements during the non-spawning season and when the fish are immature are concerned with seeking food. This movement may be more or less at random, though the number of fish of all sizes heading into creeks and up rivers to the freshwater zone suggests that lowered salinity has some attraction to the fish. Myers (1949) has suggested that it may be physiologically necessary for some fish to enter waters of varying osmotic pressure. From the occurrence of some fish at all times of the year in the saline Moreton Bay it appears that a freshwater phase is not essential for mullet. The movement upstream could be a trophic reaction to current, and such a reaction is made use of to capture mullet fry for fish farming in some countries (see Section XI).

(*b*) *Hard-gut Migration*

The hard-gut migration consists of a movement of immature fish along the beaches. The fish may come from the local river and re-enter it later; but in at least some cases these I+ and II+ fish move from one system to another, even moving south in some cases recorded from Western Australia. This class of fish is known as washout mullet in northern New

South Wales and Queensland. It is probable that in this area at least they do move out as a result of floods (Fig. 2). The effects of a flood could well be to make food scarce for a period afterwards and this would account for the "hard-gut" empty of food and explain the movement subsequent to the initial flooding out as a trophic migration.

(c) *Spawning Migration*

(i) *Down-river.*—The spawning migration begins with the downstream movement of the larger fish, which gather into schools as they go (Kesteven 1946). Roule (1915) has suggested that this is a result of lowered oxygen content of the fresh waters as the temperatures drop, but such an argument does not seem to hold in Australian waters where the oxygen content remains high (see, for example, Rochford 1953*a*, 1953*b*).

It has been suggested by Fontaine (1947) that as catadromous fish mature sexually some hormonal or similar effect prevents effective osmotic adjustment so that they are forced to move downstream. It would seem extraordinary, though admittedly not impossible, for the result of gonad ripening to have opposite effects in anadromous and catadromous fish. Certainly the migration is initiated at a time of falling temperatures, but whether this in itself could stimulate the fish to migrate is problematical.

(ii) *Exit to Sea.*—The mullet collect in ever-growing schools in the lower estuaries and then on some stimulus move out to sea. Fishermen aver that the stimulus is an offshore wind and observation records of district fisheries inspectors as related to prevailing winds confirm this (Fig. 7).

The wind data of Figure 7 were provided by the Commonwealth Meteorological Bureau, Sydney. The data are presented in three ways: hours of wind blowing from the western sector (i.e., winds recorded as from south-west, west, or north-west by the Bureau); miles run of west winds per day; and the mean speed in miles per hour of the west wind each day. It appears that the intensity of the wind is the most influential, as fish frequently move out on the first day of a strong blow but may not move at all when a prolonged but light westerly is blowing.

The times of movement of the mullet schools have been extracted from reports on fish movements submitted by the inspectors of the New South Wales Fisheries Branch. The reports are accurate to the extent that the inspectors were able to make observations regularly. Some may be based on fishermen's reports rather than the inspector's personal observation. The data for 1943 are presented as typical. Data on the years 1940-1946 are on file at the Division of Fisheries, C.S.I.R.O., Cronulla, N.S.W., but are not figured here in the interests of economy of space. No movement to sea occurred during strong or prolonged west winds during January or February when the fish were not yet ripe. A strong westerly in late March or in April certainly seems to stimulate the schools to move to sea.

However, there were always one or two reports of schools moving to sea when no strong westerlies were blowing. It is possible that the reports were biased towards the periods of west winds, as the observers might look for such movements more keenly at such times in the light of local lore on mullet. If such undue weighting can be ignored there remains evidence that more schools move to sea when strong westerlies are blowing than at other times.

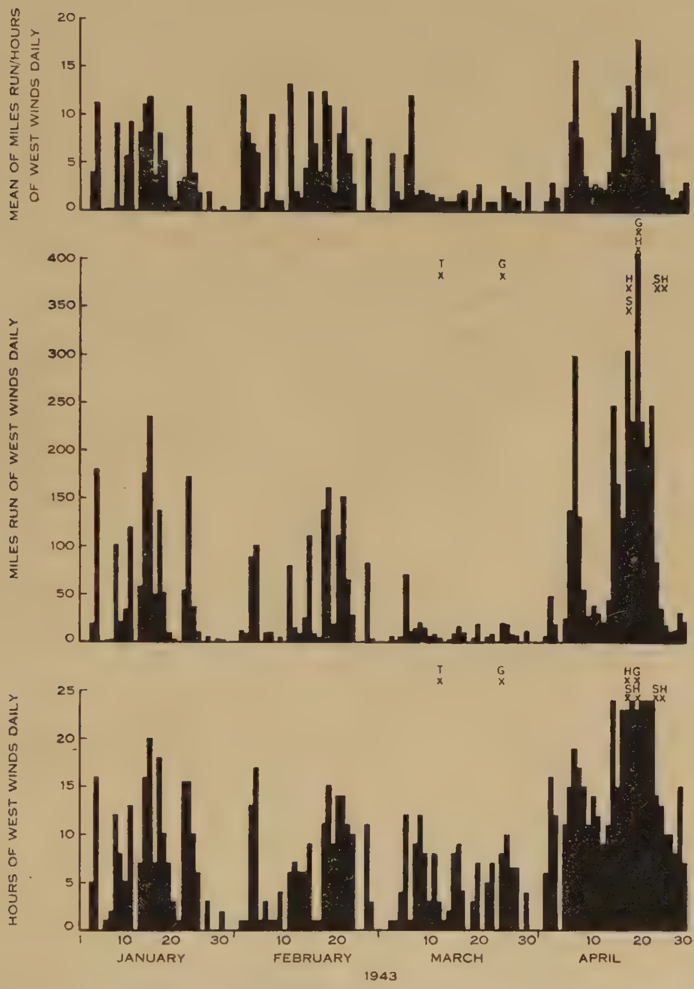

Fig. 7.—Correlation of west winds with mullet movement to sea. Upper chart, mean miles run per hour of west winds per day; centre chart, miles run of west wind per day; lower chart, hours of west wind per day. Crosses indicate days on which mullet schools moved to sea. *T*, Tuggerah Lakes; *G*, Georges River; *H*, Hawkesbury River; *S*, Lake Macquarie. Wind data, Sydney.

X. EXTRA-AUSTRALIAN STUDIES ON MOVEMENTS

It has been shown that anatomically the Australian sea mullet is indistinguishable from *Mugil cephalus*, a species of world-wide distribution in warm-temperate to tropical waters (Thomson 1954). Studies made overseas on the species may therefore confirm or add to the knowledge of the movements of this species gained in the Australian studies. The majority of such studies have been concerned with the spawning migration and entry of fry rather than local movements.

The type locality of this species was given by Linnaeus as "European seas". The species is particularly abundant in the Mediterranean and Bay of Biscay. Relevant studies have been made in France, Corsica, Italy, Egypt, and Israel. There is agreement in all accounts that *M. cephalus* leaves the rivers in autumn to spawn at sea, and that some time later (generally 4 weeks or so) the young start entering the rivers or coastal inlets in large numbers. Roule (1916) describes the movements into and from the rivers as a tropism in reaction to the presence of currents of water different in composition from that in which the fish have been. The reverse reactions, he suggests, are the result of differing reproductive and trophic needs. He repeated his earlier (1915) belief that the determining factor is the relative level of dissolved oxygen in the two waters. Kunstler (1904) states that mullet leave the Étang de Mimizan only during rain or storms. He did not state the direction of the winds which accompany such storms, but the observation is of interest in light of the movement to sea of Australian mullet with a strong offshore wind. It appears that a similar reaction is normal in Florida (Anon. 1951*a*).

The entry of the fry into the creeks against the current flow is made use of in fish farming practices at Arcachon (Arne 1938) in France, Lake Commachio and the adjacent Po River and Venice Lagoon areas (Beadle 1946) in Italy, and in Egypt (Faouzi 1938).

M. cephalus undertakes extensive migrations along the east coast of Florida according to Broadhead (1953). Idyll and Sutton (1952) found that on the west coast of Florida the migration was neither so extensive nor so definite in direction, but data on the size of the fish were not provided in either paper so that it is not known whether the fish were old enough to undertake the spawning migration between tagging and recapture. The variation in direction found by Idyll and Sutton may have been due to some juvenile wanderings equivalent to the hard-gut migration in Australia. It is interesting in this respect that Roule (1915) distinguishes between the spawning migration and an irregular migration by individuals which are either immature or adults in non-spawning condition. The difference in behaviour between mullet on the east and west coasts of Florida may be accounted for, however, by the difference in hydrological conditions. Along the east coast of Florida there is a strong current; there is no similar phenomenon along the west coast. Kesteven (1942) has explained the hypothesis that *M. cephalus* in Australian waters swims against the prevailing ocean current during the spawning migration so that the eggs and fry drift back to repopulate the rivers from which the migrating schools have come.

Rich (1926) believed that migration in North Carolina is not extensive, but Higgins (1932) believed that more extensive movement of young fish took place in New Jersey at the northern end of the mullet run, as he states that adults are never seen so far north but juveniles commonly occur there when still less than an inch long. Observations by Earll (1887) agreed with this.

There is some evidence that *M. cephalus* may occur at places distant from the coast. Whether they are there merely transiently or can remain constantly in the marine environment is uncertain. Even among the tropical Pacific islands where they are recorded (Fowler 1928) they are still within reach of freshwater streams. The species has been recorded 50 miles offshore in the Gulf of Mexico (Anon. 1951*b*). It is not recorded that specimens were actually taken to confirm the identification.

XI. The Mullet as a Migratory Type

Individual *M. cephalus* behave as catadromous fish, ascending the rivers to fresh water and going back to sea to spawn. These are diadromous fish in the sense of Myers (1949) but it is likely (Sections IV-VI and VIII above) that some of the mullet never ascend above the lower estuary, and indeed it may be that some remain always in the marine zone. The fluvial fish belong to section C of the through-running fish of Schmidt (1936), that is, trophically freshwater but generatively marine.

Those mullet which enter only into the brackish water estuaries and not, as far as is known, into the fresh water, fall into section IIB of Schmidt (as presented by Myers (1949)); that is, they are through-running trophically brackish-water fish which are generatively marine.

Heape (1931) has distinguished a gametic migration corresponding to the spawning migration of the mullet. The term "spawning" is quite distinctive in meaning and the more jargonist term "gametic" does not seem justified. Heape also defines an "alimental migration" as being a migration for self-preservation to find food. The movement of mullet in search of food around the estuaries hardly justifies the term migration, but the hard-gut migration possibly may be regarded as an alimental migration, for although it is believed that these are fish forced out of rivers by floods, the consequences of flooding are such that the fish are forced to explore for food. However, the more usually used term "trophic" may be preferable to alimental.

Myers (1949) suggests there may be another type of migration which he terms "osmoregulatory migration". He suggests that for certain fish it may be a necessity for freshwater species to spend some time in salt water and for salt-water species to spend some time in fresh water. This is not a breeding migration. Although records of such invasions are plentiful (Gunter 1938) it has yet to be demonstrated that they are in any case a physiological necessity. Certainly it would not appear absolutely necessary for *M. cephalus* to enter fresh waters. Fish of all sizes can be found in the saline lower estuaries at all times of the year.

It is apparent from the discussion earlier in this paper and from the observations of Kesteven (1953) that many mullet which have had the opportunity to travel on a spawning migration are nevertheless retaken in the rivers in which they were first tagged. If it can be assumed that the tagging itself has not interfered with the physiological rhythm of the fish then it may be assumed that the fish have in fact travelled to sea and returned, thus performing a migration in the restricted sense in which Allee *et al.* (1949) use the term. Other fish which have participated in the spawning migration evidently do not return to their former haunts but it is probable that at least some of their progeny may do so. This would be a remigration in the sense of Allee *et al.* (1949).

Therefore it is impossible to fit the sea mullet as a group into any of the classificatory schemes for migratory fish except perhaps for the general description "through-running" used by Schmidt (1936). Some individuals act as catadromic diadromous fish (Myers 1949) or as through-running trophically freshwater, generatively marine fish (Schmidt 1936). These terms can be regarded as synonymous. Others act as through-running trophically brackish-water, generatively marine fish. There is no corresponding term in the nomenclature proposed by Myers (1949).

XII. Acknowledgments

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POPULATION STUDIES ON THE TOHEROA, *AMPHIDESMA VENTRICOSUM* GRAY (EULAMELLIBRANCHIATA)

By R. M. Cassie*

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Summary

The ecology, distribution, and commercial importance of the toheroa, *Amphidesma ventricosum* Gray, are discussed. The habitat favoured by that portion of the population at present known is a beach fully exposed to heavy surf, with a fine sand and sufficient residual moisture to prevent desiccation at low tide. Frequent dense blooms of phytoplankton are necessary to provide an adequate food supply. Estimates of numerical abundance for various beaches are given, showing that violent fluctuations in numbers may occur, sometimes, but not always, with epidemic mortalities. The sampling technique for estimating numerical abundance is described and discussed.

The growth rate has been estimated for several different beaches, both by interpreting the annual growth-rings of the shell, and by analysis of length frequency data. The South Island toheroa have a significantly lower growth rate than those in the North Island. It is shown that the distribution of age classes on the beach is inconsistent with the assumption that the species is confined to the littoral region. In particular, the younger toheroa are almost invariably fewer in numbers than would be expected in a self-contained population. From this, and from the extreme fluctuations in numbers which occur from time to time, it is concluded that some part of the population is located in the sublittoral.

The spatial distribution of the beach toheroa shows a high degree of over-dispersion (or aggregation) which is mainly attributable to variations in environmental conditions. Vertical and horizontal zonation of size groups may sometimes occur, but the contributing factors are obscure. Statistical aspects are discussed in appendices.

I. Introduction

The toheroa, *Amphidesma ventricosum* Gray 1843, is described by Suter (1913) under the generic name *Mesodesma*. The genus is represented in New Zealand by four species, the remaining three being *A. subtriangulatum* Gray 1825, *A. forsterianum* Finlay 1926, and *A. australe* Gmelin 1790. These are commonly known as "pipi" but it is convenient, and more correct usage of the Maori language, to employ the name "tuatua" for the northern *A. subtriangulatum* and possibly also for the similar southern species *A. forsterianum,* reserving "pipi" for *A. australe.*

This species, considered a delicacy by the Maori, is today favoured by many white men. The other species of the genus are also considered good eating, but their smaller size makes canning scarcely profitable. The toheroa has been marketed both in New Zealand and overseas as a canned product, either as soup or as whole "tongues", which are the foot and visceral mass of the animal. Canning commenced in 1905 at Mahuta Gap on Dargaville beach, where as many as four factories once operated although only one remains today. Canning was also carried out at the Ninety-mile beach from 1923 to 1945 when toheroa became too scarce for commercial digging. Operations were transferred to Muriwai beach in 1946, after which the company's permit to dig this beach was not renewed. The total quantities canned since 1928 are given in Appendix I.

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Since the animal will keep alive for a week or more under suitable conditions when removed from the beach, it has also been sold and bartered fairly widely in the shell. However, owing to the alleged depletion of many beaches by over-exploitation, the taking of toheroas is now subject to very stringent regulations, so that today it is mainly the perquisite of the private citizen although one cannery is still in operation.

II. Geographical Distribution

Figure 1 shows the New Zealand beaches where toheroa have been recorded. On some the species may be no longer present or the range may be less than indicated, as at the Ninety-mile beach, where the toheroa has become a rarity. The two localities indicated by dots have not been confirmed recently, though there seems to be no reason for doubting the original reports. The Doubtless Bay occurrence was reported on April 22, 1937, by the "Northern Advocate" which quoted the statement of a local resident, Mr. L. J. Mathews, that toheroa had been present for short periods on Tokerau beach in 1907, 1923, 1932, and 1937. In 1938 a request was made through the Marine Department for a regulation to protect these beds. The presence on Whangape beach is assumed from a hearsay report by Mr. L. F. Ayson (Chief Inspector of Fisheries) in 1924. Mitimiti, which is adjacent to Whangape, has been known to have toheroa for many years though the numbers at times may become very small. Dargaville (or North Kaipara) and Muriwai (or South Kaipara) are today probably the principal home of the species, both having been exploited by the canning industry in recent years. Piha, one of Auckland's popular holiday resorts, is a relatively small beach and it is doubtful whether any great numbers of toheroa have ever been present there, though a few specimens from this locality are preserved in the Auckland Museum in the collection of Mr. A. W. B. Powell. Pollock, a little-known beach south of the Manukau heads, was visited by the author in 1952 to investigate reports of toheroa made by local residents. Though only one specimen was found on this occasion there is little doubt that others are present at times.

The only known occurrence on the east coast of New Zealand is at Ohope beach, near Whakatane, where sufficient numbers are present at times to be an attraction to holiday-makers. Other vague reports have been received relating to Opotiki beach a little to the east, and to Gisborne, but they have not been substantiated.

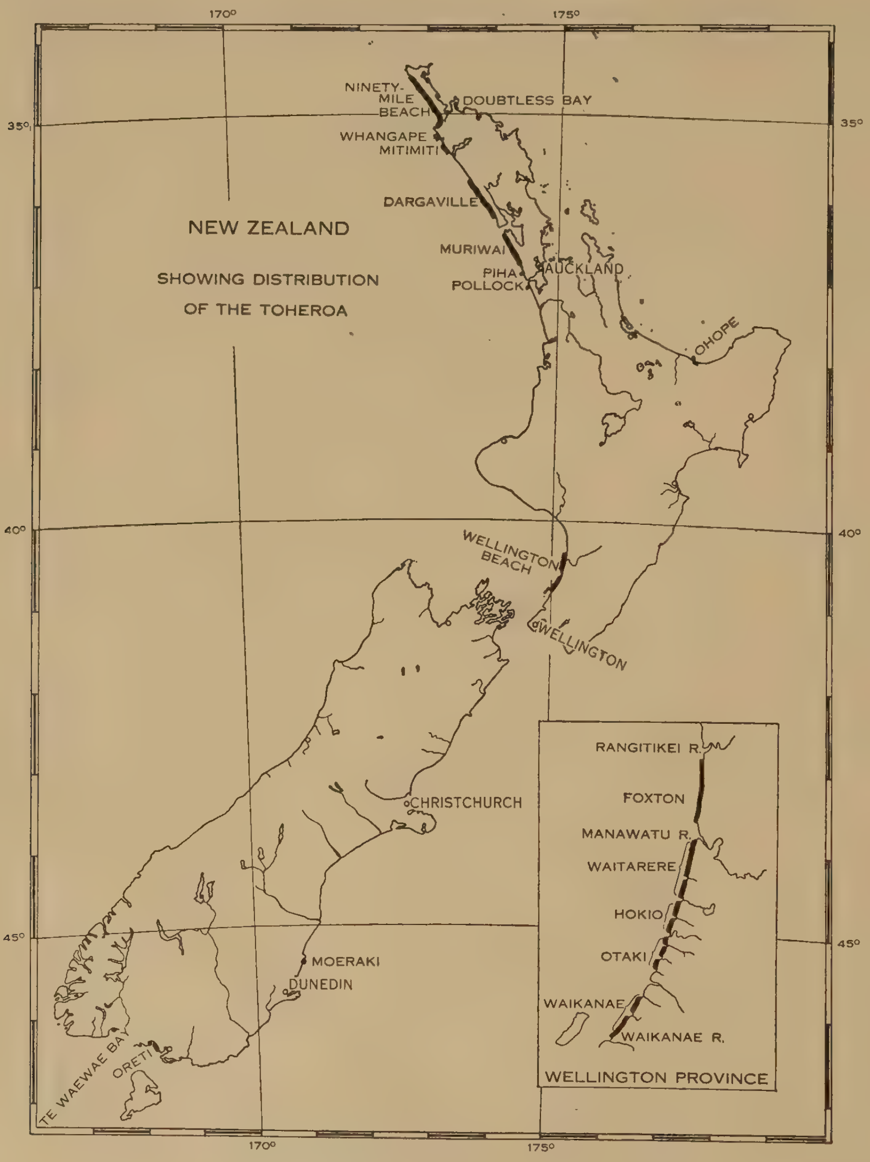
170°
175°
35°
40°
45°
NEW ZEALAND
SHOWING DISTRIBUTION
OF THE TOHEROA
NINETY-MILE BEACH
DOUBTLESS BAY
WHANGAPE
MITIMITI
DARGAVILLE
MURIWAI
PIHA
POLLOCK
AUCKLAND
OHOPE
WELLINGTON BEACH
WELLINGTON
CHRISTCHURCH
MOERAKI
DUNEDIN
TE WAEWAE BAY
ORETI
RANGITIKEI R.
FOXTON
MANAWATU R.
WAITARERE
HOKIO
OTAKI
WAIKANAE
WAIKANAE R.
WELLINGTON PROVINCE

Fig. 1.—Geographical distribution of toheroa.

From the Auckland Province there is a wide gap before toheroa are encountered again on the west coast of the Wellington Province, between the Rangitikei and Waikanae Rivers. At present the only area at all densely populated is Hokio beach, which can only be reached on foot or by a somewhat hazardous crossing of the Hokio stream by car. It is doubtful whether more than a scattered few are to be found on Waikanae beach today, though there were undoubtedly quite substantial numbers in the early 1930's. Possibly the range may sometimes extend a little further to the north of the limits indicated in the Wellington Province.

On the west coast of the South Island the toheroa is absent, probably because there are no suitable sandy beaches, but well-stocked beds are often found on Oreti (or Riverton) beach and Te Waewae Bay on the south coast. The range shown is that given in a map prepared by Ayson in 1925, though more recent inspections have indicated that the general distribution has not changed greatly since that time. One further minor occurrence in the south is recorded by Finlay (1927) and by Sir William Benham (Hefford 1930) at Moeraki (or Katiki) beach near Palmerston on the east coast, but more recent observations have not confirmed these reports.

III. General Biology

At low tide the presence of toheroa on the beach may often be readily detected by the twin siphon holes (Plate 1, Fig. 1). In larger specimens the larger or exhalant siphon hole is up to half an inch in diameter while the holes are about an inch apart. While the tide is washing over the beach, the tips of the siphons are kept level with the surface and the inhalant current is made apparent by the movement of sand particles and small organisms in the water. However, at low tide the siphons are withdrawn into the shell, which is closed as far as the gaping extremities will allow. The animal is usually found at a depth of about 6 in. if it is a large one, but nearer the surface for smaller specimens. If a toheroa is left lying on its side on the sand it is usually not long before the foot or "tongue" is protruded and inserted into the sand (Plate 1, Fig. 2), and the animal commences to bury itself, often disappearing completely within a minute.

Occasionally confusion arises in distinguishing between the toheroa and the similar though smaller tuatua which may at times be found at the same beach levels, but more usually occupying the lower littoral and upper sublittoral. The close resemblance, particularly in the very young stages, causes some difficulty in determining the geographical range from hearsay or even from published reports. However, the two species may usually be distinguished by the thicker and more glossy shell of the tuatua, together with a slight difference in shape (Plate 2, Fig. 1). In cases of doubt the more deeply indented pallial sinus of the toheroa is the best guide (Plate 2, Fig. 2).

The habitat of *A. ventricosum* is commonly considered to be confined to sandy beaches between mean low- and high-water levels (approximately), though it will be shown that there is some reason to believe it may also live in the sublittoral. On South Island beaches the lower limit may not be exposed by neap tides, but in the North Island the entire beds are usually revealed at any normal low tide. Invariably toheroa beaches are on fully exposed ocean coasts which are frequently pounded by heavy surf. The majority are on the west coast where they face the prevailing winds, though a few are recorded on east and south coasts. The beaches favoured are usually gentle in slope, varying between 1 in 50 and 1 in 25 in the mid-tidal region, while the sand itself is fine and even in texture with an average grain size of about 0.25 mm. The mineral content does not appear to be critical, ranging from the dark ironsand of Muriwai to the almost pure white silica sands of the Hokianga district. Many of the beaches, notably Muriwai and parts of Dargaville, have a gently undulating contour forming a series of alternating bays and ridges backed by foredunes, which are usually lower or completely broken behind the deeper bays. The lower levels in the bays remain wet from the receding tide and toheroa are almost invariably found in greatest density in these damp patches, being usually absent from the intervening higher levels.

Hefford (1935) suggested that the moisture to be seen at low tide was partly supplied by seepage from lakes or other sources behind the foredunes, and that this freshwater supply was essential to the well-being of the diatoms which form the principal food of the toheroa. Although this theory has been widely quoted, there appears to be little supporting evidence, and it is unlikely that these diatoms, all marine species, can be in any way related to the presence of relatively small quantities of fresh water. For the most part the toheroa appears to avoid regions near the mouths of streams and rivers, though a notable exception occurs on Dargaville beach, where the densest beds often occur where streams traverse the beach. On such beds the water, when tasted, often shows no trace of salt, though the fluid retained in the mantle cavity is by the same test quite strongly saline. Apparently, to prevent desiccation the toheroa requires a certain minimum quantity of water in the sand when the tide recedes, and within wide limits the salinity of this water is immaterial. There is no evidence that fresh water is preferred and it would seem improbable that active metabolism could proceed in a hypotonic medium.

Other beaches, notably those in the Wellington Province, lack the undulating surface found at Muriwai, and consequently there is not the same segregation into distinct beds. The distribution, though seldom if ever uniform throughout the whole horizontal range, may be more or less continuous for considerable distances. Although most beaches are backed by foredunes, either continuously or intermittently, this is not invariably the case, as many parts of Dargaville beach have high vertical cliffs behind them.

It would appear that the physical character of the beach may not be the main limiting factor in the geographical distribution, for many beaches occur, particularly in the North Island, which seem to have all the necessary features but have never been known to carry toheroa. Many attempts have been made to transplant the species to other apparently favourable localities. For instance, in 1926 about a thousand toheroa were transplanted from Muriwai to Papamoa beach near Tauranga. There is no record of any such experiment being successful, and it would appear from the wide though discontinuous range that the toheroa is well able to disperse itself, at least in the larval stages, to any suitable locality.

One biotic feature which appears to be common to all toheroa beaches is the frequent appearance in the surf of dense concentrations of algae, principally diatoms. The following genera have been identified in the gut contents of toheroa by Mr. A. S. Fuller: *Bellarochia, Rhizosolenia, Coscinodiscus, Navicula* (Diatomales), and *Phaeocystis* (Flagellata). These algae may at times form a thick, greenish brown scum on the surface of the water, visible for 100 yards or more out to sea. Heavy deposits are often formed on the beach, sometimes so thick that the slippery surface makes car driving at any speed a hazardous process. It is a widely held and apparently soundly based belief that the presence of toheroa is correlated with the presence of phytoplankton. For instance, Ninety-mile beach, which has been almost devoid of toheroa since about 1948, seldom shows the green water coloration so common on the more densely stocked Muriwai and Dargaville beaches. At the same time, the tuatua, which apparently has a similar method of feeding, is often extremely abundant on the northern beach. Some light has been cast on this difference of behaviour by Dr. J. E. Morton, who has examined the ciliary feeding mechanisms of the two species. The toheroa ingests all that comes its way in the water, and separates sand from organic material only in the alimentary canal. The tuatua on the other hand has an efficient sorting mechanism which operates *before* ingestion takes place, and is thus able to find sustenance not only from a relatively poor water-borne flora but also from dinoflagellates and other sand-dwelling species. However, when phytoplankton is scarce, the toheroa may be unable to obtain sufficient food, not because the food is absent but because it is so diluted by suspended sand that ingested material is mostly inorganic.

Although at present the hydrology of inshore waters on the west coast of the North Island is relatively unknown, Garner (1954) reports zones of upwelling near North Cape and Cape Farewell, which are on the margins of this region. If these upwellings are found to exist on other parts of the west coast they will no doubt provide a ready explanation for the phytoplankton on the beaches, while deviations of the eastern Tasman current may be responsible for the partial cessation of these blooms at times, as at Ninety-mile beach.

One particular cause of concern has been the occasional heavy mortality which may leave millions of dead and dying animals lying on the surface of the beach. The most noteworthy occurrence of this type was in January 1938, and seriously affected all the North Island beaches. It is believed that other Mollusca, such as limpets and mussels, were similarly affected at the same time. Hefford (1938) suggests that the

1938 disaster was correlated with the prevalence of easterly (offshore) winds.

Perhaps just as serious as these spectacular short-term mortalities is the gradual reduction of stocks which has apparently taken place on some beaches, particularly Ninety-mile beach, which is today almost devoid of toheroa. It has been suggested by some (e.g. Hefford 1945) that the population of this beach has been a war casualty, suffering from depredations by servicemen, crushing by heavy military vehicles, and smothering in oil from a wrecked ship. Others have blamed the operation of a commercial cannery. However, since these adverse factors were removed by the end of 1945 it would seem that other causes (e.g. the scarcity of phytoplankton) have been responsible for the failure of stocks to regenerate. It has also been suggested that the presence of large numbers of tuatua in the intertidal region of Ninety-mile beach may have been responsible for the disappearance of the toheroa (Hefford 1945; Rapson 1954). While this may be admitted as a possibility, it would seem just as probable that one species has replaced the other simply because of environmental changes. Local residents report that similar total disappearances of toheroa from Ninety-mile beach have occurred in the past, notably in 1888, 1900 (Rapson 1954), and 1917, and confidently predict that the toheroa will return in its former numbers in the near future.

IV. Condition Factor

The condition of toheroa as measured by the relationship between weight of edible meat and size of shell is a matter of some importance to the canning industry. It has not as yet been possible to collect a sufficient range of samples to determine the complete range of variation in condition factor. The high degree of variation within samples, together with the difficulty in standardizing the draining and weighing techniques of different workers, make it doubtful whether those samples which have been taken are truly representative of seasonal variations. The average weight of meat in a 4-in. toheroa may vary during the year within the range of ½ to 1½ oz.

A much more reliable guide is given by the practical experience of the cannery operators, who are in effect measuring very large samples and, during the canning season, measuring them at very frequent intervals. Mr. E. A. Meredith of Tikinui, Dargaville, has a useful measure of condition based on the number of bushels (i.e. 4-gal kerosene tins full) of toheroa in the shell required to supply 1 bushel of meat. Since in toheroa of equal condition the weight of meat is proportional to the volume of the shell,* this factor will not be affected appreciably by the size of the individual toheroa. When canning commences in about June, the condition factor is usually about 6 : 1, and improves gradually until in late August it may have reached 5 : 1 or 4 : 1. This factor prevails for 2 or 3 weeks until spawning commences, usually toward the end of September. From this time onward, condition drops abruptly to about 7 : 1 or 8 : 1.

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* It has been established that the weight of meat is proportional, without significant deviation, to the cube of the shell length. Since there is no marked allometry in shell growth, and since only a limited size range (4-6 in.) of toheroa is concerned, it would seem that the above assumption is justified.

V. Numerical Abundance

In the past, several different observers have made estimates of the number of toheroa on the more important beaches. The following information has been drawn (except where other references are cited) from Marine Department files. The first record was made in 1920 by Ayson, who reported that on Ninety-mile beach there were 54½ miles of good toheroa beds. In April 1930 (Hefford 1933) a fairly heavy epidemic-type mortality occurred and large numbers of dead and dying animals were cast upon the beach. In February 1932 a similar mortality took place, probably on a larger scale, and the numbers of dead shells were estimated by Powell as about 15 million. However, it would appear that the population had by no means been destroyed since in the following year Hefford (1933) estimated the number of living toheroa over 3 in. in length as between 11 and 12 million. The greatest density encountered in a square yard quadrat was 372, of which 224 were over 3 in. Allowing for the fact that only 30 of the 50 miles of beds were sampled and only the larger sizes counted, it would seem from the data recorded that the total number would be of the order of 30 million. About this time it is recorded that up to 1½ million toheroa were being taken annually by a canning factory. In 1938 a further heavy mortality took place throughout the whole of the west coast of the North Island. The cannery manager (Mr. McLean) reported about 20 million dead toheroa lying on the beach. Nevertheless the stocks were apparently not exhausted and Rapson (1954) estimated in November 1939 that the population was still about 12 million, while between ½ and 1 million were taken for canning. Strangely enough, the length frequencies at that time (Fig. 16(*a*)) do not indicate an unduly high number of young individuals, which might have been expected had the stocks been restored by normal processes of reproduction. Five years later Hefford (1944, 1945) considered that toheroa were scarce on the beach, but shortly after his 1945 inspection, Mr. R. G. Rule, cannery manager, reported what he considered an "amazing return" of quite well-stocked beds on sections of the beach which a few months previously had been quite bare. In 1946 Rapson estimated that the total numbers had fallen to 6 million and considered (Rapson 1952) that the beach had never before been so barren. By 1948 the numbers had been reduced to such an extent that Rule, after examining some 33 miles of beach, was able to find only one living specimen, while the author had a similar experience a little later in the same year. Occasional reliable reports have since been received of the finding of small numbers of toheroa, but for the most part the species which was once counted in millions appears to have almost disappeared.

Passing southwards, the next beach of interest is Mitimiti, which is even today rather difficult of access and is frequented mainly by the local Maoris who have jealously guarded, and as far as possible controlled, the taking of toheroa. No estimate of the total numbers is recorded prior to 1948, but it would appear that this comparatively short beach has never contained numbers of comparable magnitude to, say, Dargaville beach. In 1924 Ayson reported fairly scanty stocks and similar conditions apparently prevailed when Captain C. Daniel, then District Inspector of Fisheries, Auckland, made an inspection in 1943. In September 1948 the author made a quantitative survey and estimated the numbers at 10,000. At this time a truckload of visiting Maoris was observed to remove at least 1000 toheroa in one day. In November of the same year the local Honorary Inspector of Fisheries, Mr. Hipiriona Hotere, reported that about 20 similar truckloads per month had been removed since the author's visit. Mr. S. Hayden estimated that 8000 toheroa had been taken in 1 day. Very little information is available for the next few years except for occasional local complaints of the shortage, but in spite of the above depletions, in 1954 Mr. A. H. Taylor, Inspector of Fisheries, found toheroa once again present in numbers comparable with those in September 1948.

Although commercial canning operations have been more or less continuous on Dargaville beach since 1905, the total population appears to have defied any accurate numerical estimates. In 1938 Rapson (1954) estimated the total population at 9 million while the author 10 years later estimated it at about 5 million. Owing to the extremely variable nature of the distribution of beds it is likely that both estimates are subject to considerable error. Comparatively sudden fluctuations either in numbers or in size composition seem to be common on this beach, but it is impossible to be certain whether these occurrences represent any actual change in total numbers, rather than a movement of toheroa from one part of the beach to another.

The most complete set of records available are those for Muriwai beach. Hefford (1927-1945) frequently mentions this beach and further data are held on Marine Department files. Table 1 gives a summary of these records.

It is not known precisely what methods were employed before 1947, but it would seem that in most cases only a few days were available for the survey, so that the intensity of sampling must have been fairly low. Nevertheless if due allowance is made for a relatively high sampling error all estimates appear to have some degree of consistency, and the stocks have remained within the limits of 5 and 15 million without significant change being detected, with the one exception of the period immediately following the 1938 mortality, when a drastic reduction in numbers undoubtedly occurred. Nevertheless in spite of this setback the stocks have made a rapid recovery. Here, as with Ninety-mile beach at about the same time, it is difficult to imagine how the numbers could have been restored so quickly if repopulation depended entirely on the reproductive capacity of the survivors. The size distribution at the end of 1939 (Fig. 16(*d*)) differs very little from other years, and there is no predominance of young individuals.

TABLE 1

SUMMARY OF NUMERICAL POPULATION ESTIMATES, MURIWAI BEACH

Date	Estimate	Made by	Remarks
	(× 10^6)		
1937	15	A. M. Rapson	See Rapson 1954
1938	4	A. M. Rapson	Before heavy mortality
1938	<1	A. M. Rapson	After heavy mortality
1940	5	A. M. Rapson	
1941	5	A. M. Rapson	
1942	10	A. M. Rapson	Recorded as 5 million over 3 in. in length
1943	>5	A. E. Hefford	Between 15 and 25 miles north of entrance. Total probably about 10 million
1947	>3	A. C. Kaberry	Between 16 and 26 miles north of entrance. Total probably about 6 million
1948 (July)	10	R. M. Cassie	
1948 (Dec.)	13	R. M. Cassie	
1949 (June)	15	R. M. Cassie	
1950 (July)	>1	R. G. Rule	Less than half the beach surveyed; only shells more than 3½ in. long counted. Total probably at least 5 million
1952 (Aug.)	8	M. K. McKenzie	

In the Wellington Province it is possible to trace the history of Waitarere beach to some extent. In 1935 Mr. M. W. Young, then Fisheries Biologist, Marine Department, recorded a number approaching 2½ million for this beach. In 1940 Rapson (1954) estimated about the same total number of toheroa over 3 in. long for all beaches between Waikanae and the Manawatu River. In more recent inspections made by the author and others it is doubtful whether the numbers have been even as high as 0.1 million. However, on Hokio beach immediately to the south of Waitarere it seems that the population still maintains a moderate strength, being about 0.7 million in 1948. This would appear to be the last remaining stronghold of the toheroa in Wellington Province.

No quantitative studies are available of the South Island beaches, but apparently there have been some fluctuations either in abundance or in dispersal, as witnessed by Ayson, who reported in 1925 that toheroa had extended their range on Oreti beach to about 10 miles, about twice the distance found less than a year previously.

VI. SAMPLING TECHNIQUE

The sampling unit employed in 1948, a quadrat 2 ft square, was dug with a flat-pronged, 7-in. garden fork. Quadrats were at intervals of 15.9 ft in "traverses" extending from the upper to the lower edge of the beds at right angles to the coastline. In the July survey of Muriwai these traverses were at first spaced at intervals of 87 ft (paced out parallel to the coastline), but after the first 16 miles of the beach (as measured from the entrance at the south end) the interval was increased to 172.5 ft. From 1949 onwards the traverse was replaced by a continuous belt transect one fork width (i.e. 7 in.). Transects were divided into units of 15 ft, while the paced intervals (165 ft) were retained as before. The belt transect method was found more convenient to operate, particularly on very wet sand, although the quadrat has certain merits which will be discussed in Appendix II.

In surveys of Muriwai beach it has not been found necessary to sample quantitatively the whole length of the beach since the toheroa are almost always congregated in distinct and easily recognizable beds. The southern end of the bed was picked visually and the first traverse or transect was dug at half the normal sampling interval from this end. The same principle was employed in choosing the position for quadrats, digging commencing at the upper edge of the bed and continuing at the specified intervals until no further toheroas were found. It was usually possible to determine by the presence or absence of siphon holes (Plate 1, Fig. 1) whether any toheroa were present, but if any doubt arose further quadrats were dug at the standard intervals above or below the apparent edge of the bed. It is possible that on some occasions the extent of the bed was underestimated, but it is unlikely that toheroa in densities more than 1/sq. yd were neglected except in rare cases. With average densities of 24/sq. yd (Muriwai, July 1948), even if (to take a fairly pessimistic estimate) one quadrat in five were omitted in this way, the negative bias so introduced would be no more than 1 per cent., which is small compared with the sampling error.

In computing the estimate of the total population the total number of toheroa dug was multiplied by a factor:

Area of quadrat/(Interval between quadrats
× Interval between traverses),

or:

Width of transect/Interval between transects.

The actual factors employed for Muriwai are shown in Table 2.

Although no quantitative samples have been recorded outside the apparent limits of the bed, extensive exploratory digging has been carried out above, below, and between beds in an effort to locate the smaller toheroa, which are normally scarce or absent in the main beds.

TABLE 2

CONVERSION FACTORS AND SAMPLING INTENSITY OF POPULATION ESTIMATES, MURIWAI BEACH

Date	Range (miles)	Factor	Sampling Intensity (%)
July 1948	0-16	$(87 \times 15.9)/4 = 345.8$	0.29
	16-28	$(172.5 \times 15.9)/4 = 685.7$	0.15
June 1949		$165/0.583 = 283.0$	0.35

VII. SPATIAL DISTRIBUTION

It is quite evident that toheroa are not dispersed at random over all parts of the beach, but that environmental conditions are largely responsible for the characteristic distribution. Upper and lower limits are clearly defined and obviously correlated with tidal range. On a horizontal scale, beds are often delimited by changes in the contour of the beach, while even on apparently continuous beds density usually fluctuates with variations in moisture content of the sand at low tide. The largest numbers are almost invariably to be found toward the centre of the bed, both vertically and horizontally. In an analysis of the Muriwai survey of August 1952 an average of 70 per cent. of the toheroa were found to occur in the second and third quarters of the vertical range. Out of 17 beds examined, only one showed significantly less than 50 per cent. in this central range, while in one bed the proportion was as high as 85 per cent.

For purposes of a sampling census it is necessary to treat the population as a highly over-dispersed (or aggregated) one, calling for a different statistical treatment from that which would apply if the distribution were random. The statistical aspects of spatial distribution and sampling technique are discussed in Appendix II.

VIII. GROWTH RATE

Two previous workers have made estimates of the growth of the toheroa. Hefford (1927, 1928) considered that the average annual increase in length on several North Island beaches was approximately 1 in. This value presumably refers to the early years of the toheroa and implies a fairly wide margin of error, in which case the estimate is not incompatible with those of later workers. Rapson (1952) gives tables of mean growth rate, derived from shell readings, for five different beaches, and also several estimates for Muriwai and Dargaville based on length frequencies. Some of this data will be considered below. In a previous paper (Cassie 1951) the author has described the growth in length as being proportional to the square root of the age. For Muriwai the appropriate equation would be:

$$\text{Length in inches} = 1.9\ (\text{age in years})^{\frac{1}{2}}.$$

This has proved a useful empirical formula, but as it has no basis in any law of growth it has since been discarded. The relationship does not hold after the first 5-7 years.

Two methods of age determination have been employed, viz. length frequency and shell reading. The initial data for length frequency determination are obtained when making surveys of toheroa beaches for population estimation. Measurements of maximum shell length were at first taken to the nearest quarter-inch, on a flat board similar to that used in measuring fish. However, during the Muriwai survey in July 1948 it was found that the markings on the board tended to be obscured by sand. Accordingly a new type of board was constructed which removed this difficulty and at the same time permitted measurements to be made to the nearest 0.1 in. (Fig. 2). The inside dimensions are approximately 20 in. long by $2\frac{1}{8}$ in. high at the broad and $\frac{1}{2}$ in. high at the narrow end, while the width corresponds to the scale markings on the far edge. The toheroa is slid in from the right-hand end until it will go no further, being held with its central plane vertical and perpendicular to the far wall of the board. The measurement is then read off against the junction of the shells on the scale. The few shells under an inch in length have been measured separately in the laboratory.

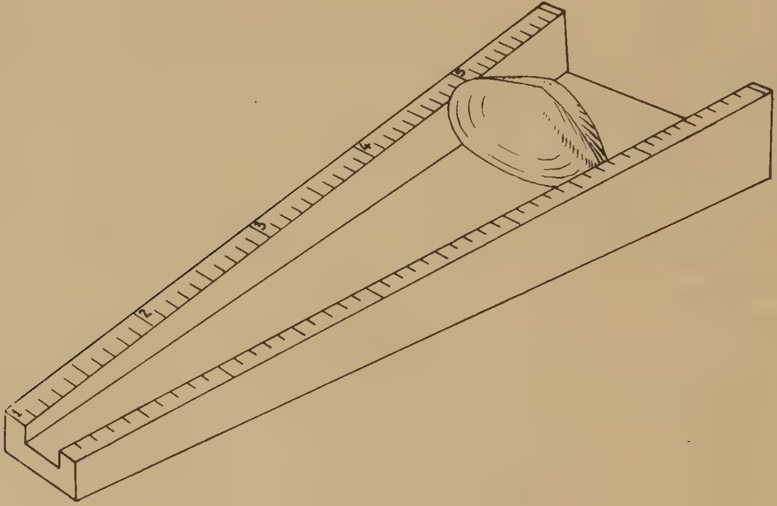

Fig. 2.—Toheroa measuring board.

The data so obtained are discussed more fully in Section IX. The length frequencies were analysed by the method described in previous papers (Cassie 1950, 1954). Although in some cases no distinct size modes could be separated, nevertheless it has been possible, where smaller sizes have been more abundant, to distinguish and to compute parameters for at least the first two age classes.

The shell-reading technique depends on the fact that the concentric growth markings of the shell exhibit alternating light and dark regions which appear to be annual in occurrence. Since the shell grows by additions both to the edge and to the inner surface, this periodic structure is shown, not only on the surface of the shell but also in a ground and polished section (Fig. 3). It is also to be seen (Fig. 4) in the adductor and retractor muscle scars (*a.a.s.*, *p.a.s.*, and *m.r.s.*), the resilium depression (*res. d.*), and the broken ends of the resilium itself. Figure 3 is a diagrammatic representation of a sectioned shell, the thickness being exaggerated. By reflected light the lighter zones appear white, while the darker zones (black in the figure) have a translucent, vitreous appearance. The darker zones become apparent on the surface of the shell as fine concentric grooves or

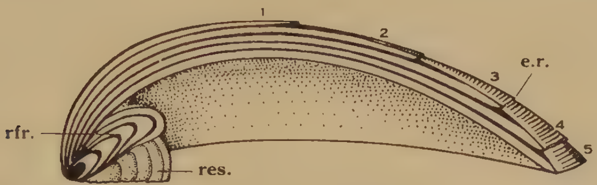

Fig. 3.—Transverse section through umbo of toheroa shell, showing annual growth rings. 1-5, Summer growth rings; *rfr.*, resilifer; *res.*, resilium; *e.r.*, external (winter) growth ring.

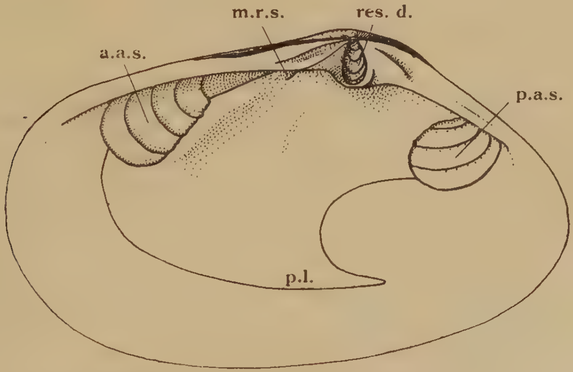

Fig. 4.—Inner surface of toheroa shell, showing annual growth rings. *a.a.s.*, *m.r.s.*, *p.a.s.*, Adductor and retractor muscle scars; *res. d.*, resilium depression; *p.l.*, pallial line.

external rings (*e.r.*) which are usually more obvious toward the margins of older shells. About midway between these grooves a lighter-coloured ring (1, 2, 3, etc.) is sometimes evident on the surface. This, however, is better viewed by bright transmitted light, when it shows clearly, being more translucent than the remainder of the shell. The internal periodic structure is shown particularly clearly in the section of the resilifer (*rfr.*) and sometimes also in the resilium (*res.*).

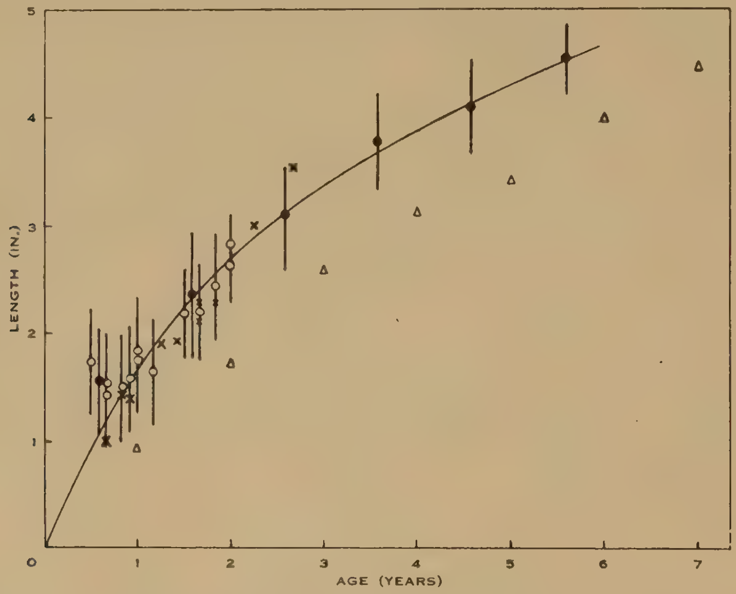

Fig. 5.—Length-age relationship, Muriwai. Vertical lines represent a 95 per cent. probability range of size.

● Combined length frequencies and shell ages, July 1948.
○ Length frequencies.
× Length frequencies (Rapson 1952, Tables 7 and 8).
△ Shell readings (Rapson 1952, Table 9).

By the examination of shells taken at different times of the year it has been established that the light zones represent summer and the dark zones winter growth. Since the toheroa spawn in the summer (often about November or December) the presence of a light zone represents the completion of approximately 1 year's growth. As might be expected, the summer rings are relatively broader, particularly in the young toheroa. After 5-7 years there is usually an abrupt discontinuity in the spacing of the rings, the intervals becoming narrower.

For determination of age the annual structures may be employed in two ways. Firstly, each individual may have an age assigned to it using all sources of evidence to be seen in the shell. Data obtained in this way will be referred to as *shell ages*. In addition, however, each shell carries a record of its past growth, from which the length at each successive year can be measured. This is equivalent to the back-calculation of lengths from fish scales, but has the advantage that no proportional calculations need to be made, since the actual margin of the shell in a previous year can be determined, and its length measured directly. Data obtained in this way are referred to as *shell readings.* Whenever possible the summer rings have been employed for this purpose. Although rings are relatively broad, the centre as seen by transmitted light is sufficiently narrow for length measurements to the nearest 0.1 in. to be taken with consistency. The assumption that the summer ring represents the completion of a year's growth is borne out well by comparison with length frequency determinations. In doubtful cases a check has been made on the shell reading by grinding a section or by interpolating between winter rings. The month of December has been taken as an arbitrary birth date, though there is evidence that the spawning season may last longer than 1 month.

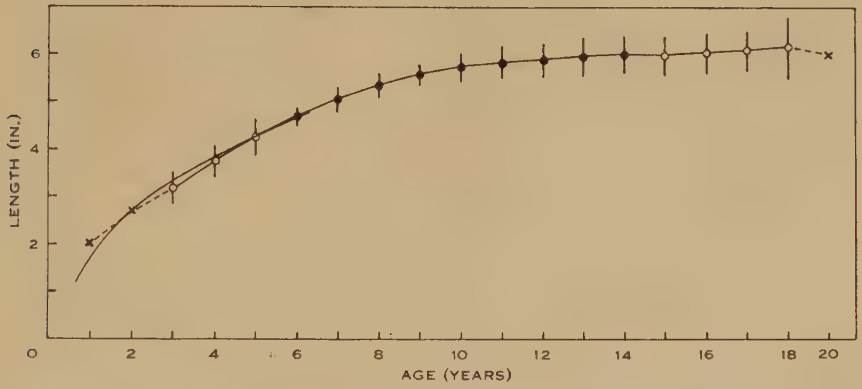

Fig. 6.—Length-age relationship from shell readings of subfossil toheroa, Muriwai. Curve of Figure 5 is superimposed for comparison. Vertical lines represent a 95 per cent. probability range of size.
● $n > 12$; ○ $n < 12 > 3$; × $n < 3$.

A summary of the available data is given in Appendix III and Figures 5-10. Data given by Rapson (1952) have been included for comparison. It will be noted that his shell readings (white triangles) do not agree with the main curves in Figures 5, 7, and 8 though lying parallel to them. It is perhaps significant that a displacement of 1 year either to right or to left will correct this discrepancy in each case. The most complete set of information is that for Muriwai beach (Fig. 5). The vertical lines through certain points represent a 95 per cent. probability range of size. The standard error of the mean is in all cases small enough to be neglected. The curve drawn through the points has been fitted by eye to serve as a frame of reference for comparison of data from other sources. It will be seen that both the means determined from a combination of length frequency and shell age determinations (black circles) in 1948 and those obtained from an assortment of length frequency determinations alone (white circles) are consistent with the curve except near the lower extremity of the length scale, where a number of points have a higher value than would be expected. This may be due to the fact that spawning commences somewhat earlier than December, but it is believed that some of the discrepancy is contributed by a selective bias, either in sampling, or more probably in the actual occurrence of the "0+" age class on the beach. It would seem that often the young toheroa do not become evident until they reach about an inch in length.

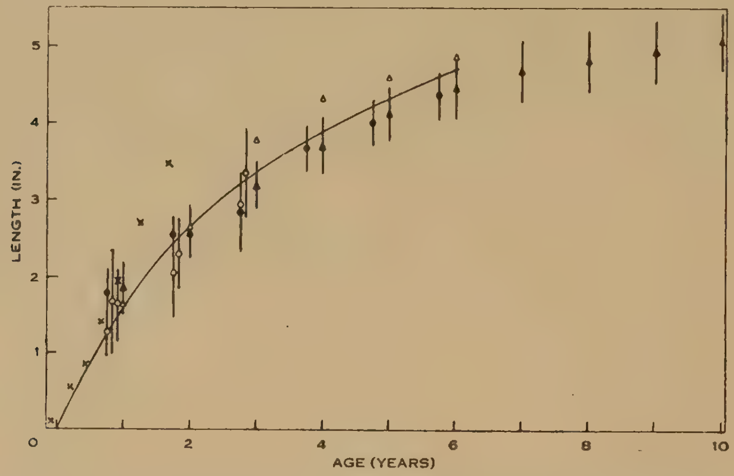

Fig. 7.—Length-age relationship, Dargaville. The Muriwai curve (Fig. 5) is superimposed for comparison. Vertical lines represent a 95 per cent. probability range of size.

● Shell ages, September 1948.
▲ Shell readings, September 1948.
○ Length frequencies.
× Length frequencies (Rapson 1952, Table 6).
△ Shell readings (Rapson 1952, Table 9).

Figure 6 gives the mean shell-reading curve for a sample of 13 large dead toheroa shells taken from above high-water mark at Muriwai in July 1948. These abnormally large shells, which may or may not be recent in origin, are discussed further in Section XII. The first few years' growth is difficult to estimate since the early rings are obscure. Nevertheless the growth appears to agree well with the curve from Figure 5, which has been superimposed for comparison. The decline in apparent growth rate after about 7 years is very noticeable. If the shell readings are to be believed, many of these outsized molluscs have lived to the age of about 20 years. Live animals found on the beach rarely give so high a value, though 15 years is apparently not an uncommon age.

Figure 7 summarizes the information for Dargaville, plotted as before against the Muriwai curve. The data from shell readings (black triangles), shell ages (black circles), and length frequencies (white circles) are consistent with a growth curve slightly lower than but parallel to that of Muriwai.

In Wellington Province a series of data from length frequency analysis (Fig. 8, circles) can be fitted reasonably well to the general shape of the Muriwai curve, falling slightly below it as might be expected for a more southern beach, although the difference is by no means conclusive.

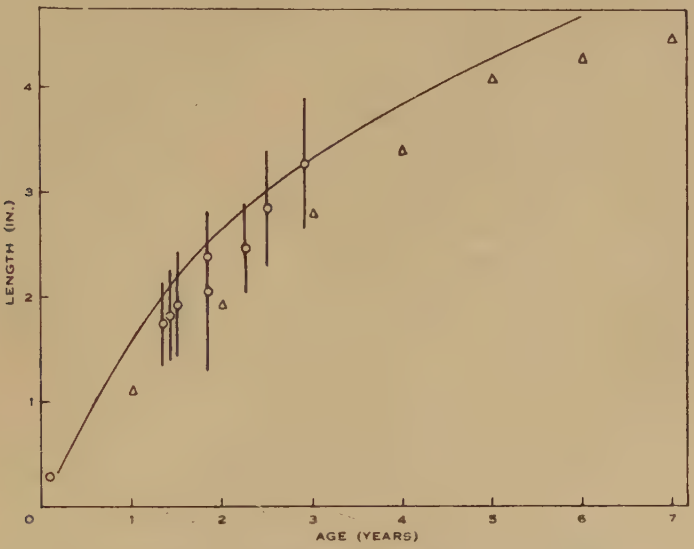

Fig. 8.—Length-age relationship, Wellington Province. The Muriwai curve (Fig. 5) is superimposed for comparison. Vertical lines represent a 95 per cent. probability range of size.

○ Length frequencies.

△ Shell readings (Rapson 1952, Table 9).

Figure 9 shows shell readings from a small sample taken from Ohope beach. The fiducial limits of the mean ($P = 0.05$), which are relatively broad in this case, are indicated by slightly heavier vertical lines. It would appear that the growth curve is very similar to that of Muriwai, though the exact agreement is probably a coincidence.

Shell readings from Oreti beach in the south are represented in Figure 10. In this case the growth is undoubtedly very much slower than for Muriwai, which is not surprising since the two beaches are separated by nearly 10 degrees of latitude. This is borne out by the relatively small maximum size reached by the South Island toheroa.

It will be seen from the above data that two independent sources of age determination have given consistent results, although the confidence limits of the various sets of information are probably too great and the data too heterogeneous to permit the fitting of any precise mathematical curve. The discrepancies between the values given by the author and by

Rapson (1952) can usually be reconciled by displacing one or the other set of points by 1 year. However, it will be seen below that, even within the relatively wide limits of confidence imposed by these discrepancies and by the variability of the data, it is still possible to draw some very significant conclusions regarding the age distributions in the various populations.

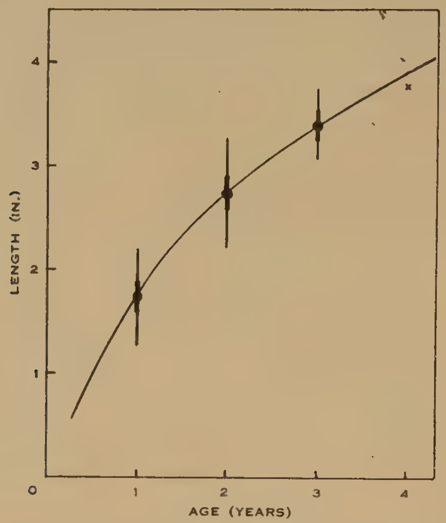

Fig. 9.—Length-age relationship from shell readings, Ohope. The vertical lines represent a 95 per cent. probability range of size, and the heavier vertical lines the fiducial limits ($P = 0.05$) of the mean.

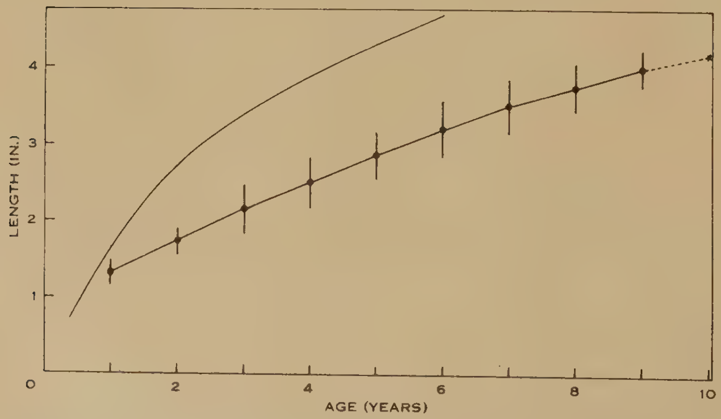

Fig. 10.—Length-age relationship from shell readings, Oreti. The Muriwai curve (Fig. 5) is included for comparison (upper curve). Vertical lines represent a 95 per cent. probability range of size.

IX. Age Composition of Population

As mentioned in the previous section, a record of lengths of all toheroa dug has been kept throughout these investigations. When this information is plotted in histogram form it is difficult to find any distinct pattern of variation, either in time or in space. In some, but by no means all, cases it is possible to distinguish some of the earlier age groups. As a rule the modes are more distinct when only a small section of a beach is represented.

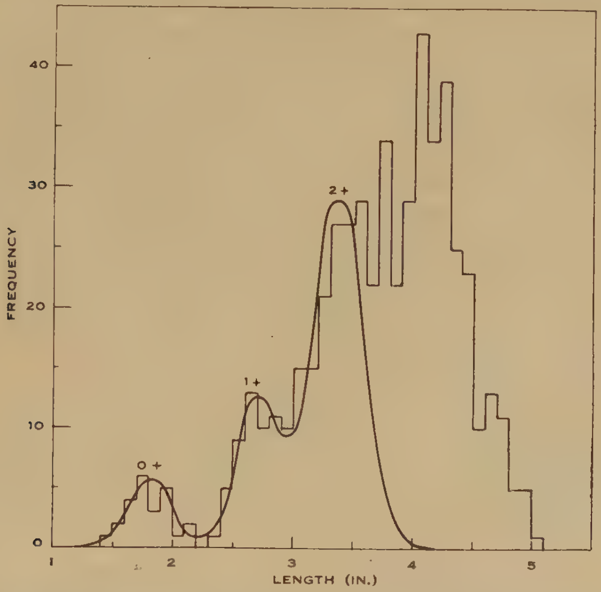

Fig. 11.—Sample length frequency distribution dissected into age classes (Muriwai, December 1948). Histogram, actual length frequencies; curve, expected population frequencies for first three age classes.

The modes have a tendency to vary slightly in position in different sections of a large beach such as Muriwai, so that when all the data are pooled the "age groups"* tend to be obscured. A sample distribution is shown in Figure 11. Two distinct modes are apparent, representing the "0+" and "1+" year classes respectively. At least three other modes can be distinguished, but only one of these has been interpreted as an age group (2+), and even this must be treated with caution, since it is often possible to obtain more than one equally acceptable solution to the more complex parts of the distribution (cf. Harding 1949, p. 149). Whenever it has been considered valid to do so, the frequency distributions have been dissected into the component age groups by the probability paper method

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* The assumption that these are truly age groups has been borne out, it is believed, by the general agreement of the mean lengths of these classes with the growth curves determined by shell readings.

(Cassie 1950, 1954). The details of the solution and of the test of goodness of fit for the data portrayed in Figure 11 are given in Appendix IV. The low value of χ^2 ($P > 0.5$) indicates that for the size range tested the solution is an acceptable one. The expected population curve is superimposed on the histogram for comparison with the sampling data. All parameters attributed to "length frequency ages" in Appendix IV have been determined in this manner.

TABLE 3

DISSECTION OF LENGTH FREQUENCY DATA, MURIWAI, JULY 1948

Age Class (yr)	$f\%$	$\bar{x}$	s	x
0+	3.7	1.55	0.25	1.1
1+	21.7	2.36	0.29	2.3
2+	28.8	3.02	0.25	3.1
3+	29.6	3.55	0.24	3.7
4+	21.2	4.00	0.20	4.1
5+	4.0	4.42	0.21	4.5
6+ and over	1.0	—	—	—

If no information beyond the length frequencies is available, the probability paper technique can only be applied to the earlier age groups where the modes are readily distinguished. However, given a knowledge of the mean growth rate, it is possible to carry the dissection on into the later age groups, by estimating mean lengths from the growth curve, and interpolating points of inflexion (corresponding to minima on a histogram) between them. By slight adjustments of the estimated means it is possible to obtain a solution which gives a reasonably accurate picture of the age distribution. This has been done for the pooled data from Muriwai (July 1948), a sample containing over 18,000 toheroa. The results are given in Table 3, where $f\%$ is the percentage of the total in each age class, $\bar{x}$ and $\bar{s}$ are the mean length and standard deviation respectively from the probability paper solution, and $\bar{\mathrm{x}}$ is the expected mean length from the growth curve in Figure 11.

It is not possible to apply the standard tests for goodness of fit to this solution, since the pooling of samples has introduced heterogeneity into the age groups. For instance, the 0+ group is drawn, not from one population with a mean of 1.55 in., but from a number of such populations, the means ranging from 1.2 to 1.9 in. However, three complementary points of evidence suggest that the analysis has been sufficiently faithful to show at least the gross features of the age composition. Firstly, the length frequency distribution of the model is similar in form to the data; secondly, the mean lengths $\bar{x}$ of the age groups agree well with the growth curve x, which has been determined by independent means; while finally, the standard deviations are very nearly constant. To satisfy any two of these requirements, quite a number of different solutions would perhaps have served as well, but it is unlikely that any more than minor variations of the one solution would satisfy all three.

The immediate impression gained from this table is that there has been particularly poor recruitment of young individuals in the last year, and particularly good recruitment four (3+) and five (4+) years back. If this is the case, it might be expected that the progress of age groups of such widely different strengths could be followed by examining the size distributions both of previous and of subsequent years. Referring now to Figure 12, which portrays length frequencies over a period of years (including July 1948), it is seen that no such regular sequence can be traced.* Throughout the whole series there is a consistent paucity of toheroa in the first two or three age classes and a dominant mode always in the neighbourhood of 3 in., corresponding roughly to either the 2+ or

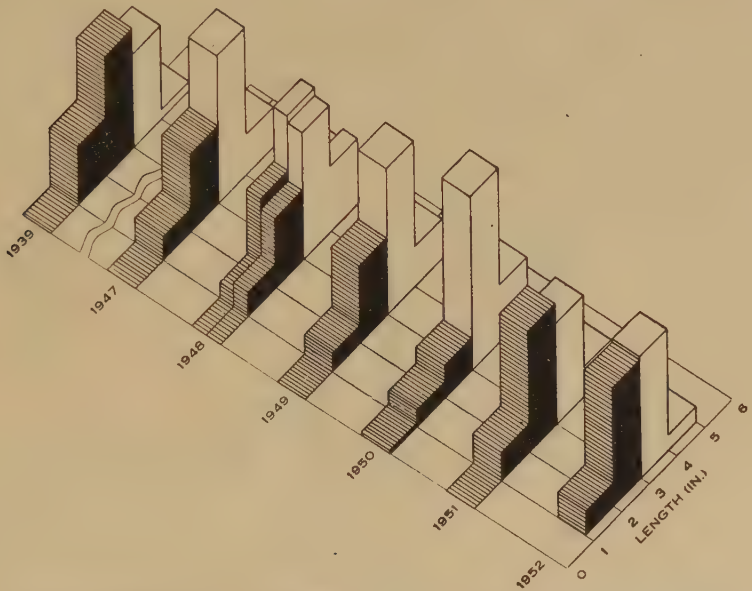

Fig. 12.—Muriwai, percentage length frequency, 1939-1952. Shaded areas, toheroa less than 3 in. (Two sets of samples were taken in 1948, i.e. July and December.)

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* The dates and total numbers of toheroa measured for each histogram are as follows: Oct. 1939, 1447 (Rapson 1952); Aug. 1947, 12,895; July 1948, 18,345; Dec. 1948, 2155; June 1949, 7136; Feb. 1950, 4720; Nov. 1951, 4308; Aug. 1952, 19,720.

In order to present a clearer picture, 1-in. class intervals have been employed instead of the finer groupings of the original data. However, the raw data, though somewhat more complex in appearance, does not in any way alter the following conclusions. Recent examination of an old field notebook belonging to Mr. A. E. Hefford reveals that a similar type of distribution existed as far back as 1927.

the 3+ age class. In Figure 13 the available data from 1947 to 1952 have been pooled and dissected into age groups,* producing very much the same type of distribution as for 1948 alone except that many of the irregularities have been smoothed out.

It is usually to be expected that the mean age distribution over a period of years will show the age classes arranged in descending order of strength from left to right, describing a curve of the exponential type. This is clearly not the case here. In fact the first three year classes form an ascending series. It is just possible that the 0+ group is under-represented in sampling owing to the smallness of the individuals, but it is most unlikely that 1+ shells (averaging over 2 in. in length) would be any harder for the digger to locate than 2+ shells (averaging about 3 in.). Since 3-year-old animals cannot materialize *de novo* without first being 1- and 2-year-olds it must be concluded that the toheroa sampled on Muriwai beach are not a self-contained population and must be in communication, at least intermittently, with toheroa in some other region which is not represented in the samples.

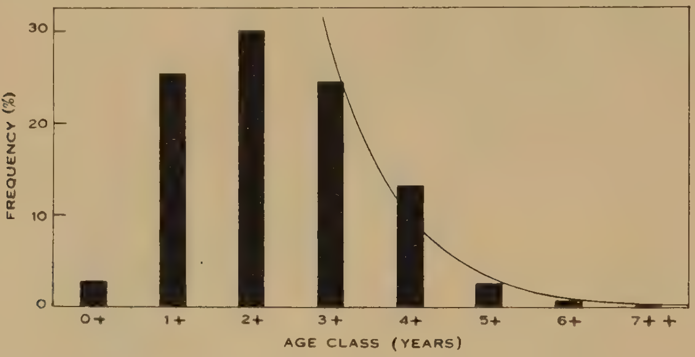

Fig. 13.—Muriwai, 1939-1952, percentage frequency of age classes. Note divergence of age distribution from exponential curve.

There is a further anomaly, though less evident, in the frequency of the later age classes. The relative frequencies together with the apparent instantaneous annual mortality rate from 2+ years onward are shown in Table 4. Such an acceleration of mortality rate, though not fundamentally impossible, does not seem probable. If the above rates were carried to their logical conclusion, no toheroa would survive beyond 9 or

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* Dates and total numbers are as follows: May 1933, 197; Nov. 1934, 1405; Nov. 1935, 1229; Apr. and Oct. 1940, 935 (Rapson 1952); June 1948, 798; May 1949, 487; Nov. 1951, 396.

Since data from a number of different years and seasons have been pooled, it is obvious that no modes will be evident, so that the probability paper technique cannot be applied to any advantage. In Figures 13 and 15 the analysis has been carried out simply by partitioning the frequencies at yearly intervals from the growth curve in Figure 5.

10 years. This is contrary to the evidence supplied by shell age determinations, which sometimes indicate a longevity of at least 15 years. In Figure 13 a logarithmic survival curve has been fitted to the frequencies from 3+

TABLE 4

APPARENT INSTANTANEOUS MORTALITY RATE, MURIWAI

Age Class (yr)	Frequency (%)	Annual Mortality Rate
2+	30.0	0.20
3+	24.5	0.63
4+	13.1	1.26
5+	3.7	1.78
6+ and over	0.08	2.05

to 6+ years, giving a mean instantaneous mortality rate of 1.23 (about 70 per cent.) per annum which in itself seems an unduly high value.

A similar conclusion is reached even more decidedly in considering the Wellington Province beaches. Figure 14 shows the size distribution on the Hokio beach at various times between 1933 and 1951. Here again there is a consistent pattern of distribution, while the paucity of the smaller sizes is even more marked. The principal mode is invariably

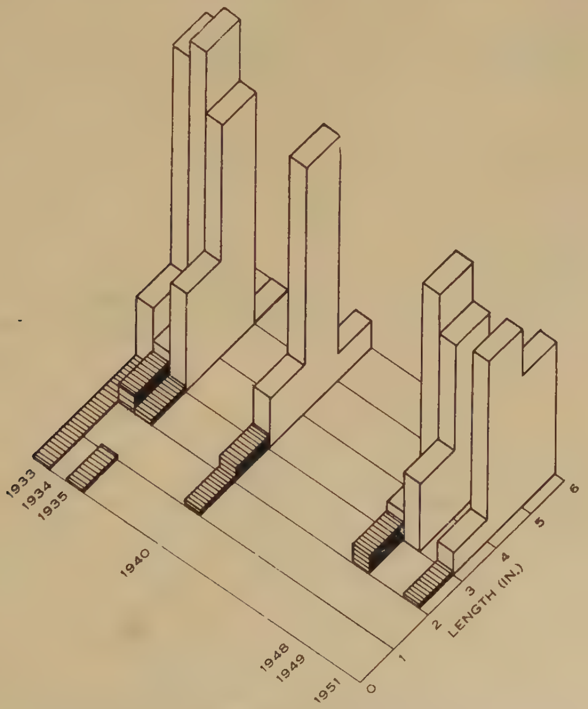

Fig. 14.—Hokio, percentage length frequency, 1933-1951. Shaded areas, toheroa less than 3 in.

between 4 and 5 in., while the proportion of toheroa under 3 in. in length is seldom more than 5 per cent. Pooling and dissecting into age groups as before, using a growth curve derived from Figure 5, gives the frequency diagram in Figure 15. A slowly ascending series of frequencies is shown, culminating with over 50 per cent. of the sample 7 or more years of age, and with the 0+ group not represented at all.

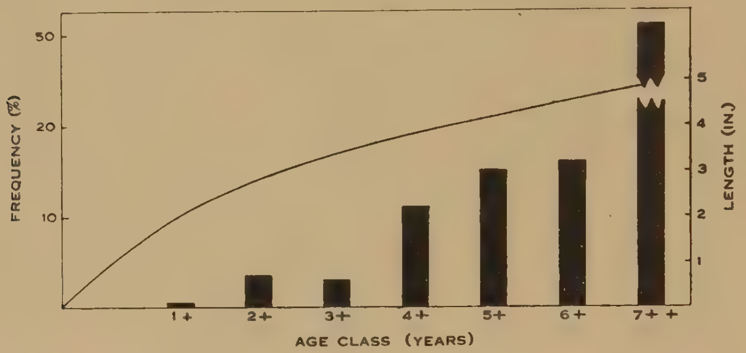

Fig. 15.—Hokio, 1933-1951, percentage frequency of age classes. Growth curve of Figure 5 is included for comparison (right-hand scale).

It will be noted that the age composition given by Rapson (1952, Table 10) is at variance with that shown in Figures 13 and 15. Furthermore, if the method of derivation quoted (Weymouth, McMillin, and Rich 1931) is applied to Rapson's own data (viz. Table 9 and appendices) it is not possible to reproduce the data in his Table 10. For instance, it would seem that for Muriwai the distribution of successive ages should be: 1 year, 0; 2 years, 195; 3 years, 620; 4 years and over, 562.

X. CLASSIFICATION OF SIZE DISTRIBUTIONS

Some further examples of length distribution from various beaches are given in Figure 16. Besides illustrating several miscellaneous sets of data not previously presented, these figures serve to illustrate the manner in which the distributions from various beaches may be classified. Broadly speaking, two types may be distinguished. The first, which might be described as the "Muriwai type", is seen in Figures 16(*a*) and 16(*d*) (Ninety-mile beach, November 1939, and Muriwai, October 1939, both from Rapson (1952)). A single principal mode occurs somewhere about 3 in. and a fairly broad range of sizes is represented both above and below the mode. The data available for Ninety-mile beach may not, however, be sufficiently representative for classification, since various references have been found (Marine Department files; Rapson 1954) to the predominance on this beach at certain times of toheroa under 3 in. in length. The second or "Wellington type" has a fairly narrow principal modal group close to 5 in., while smaller toheroa are either absent or represented only by one or more relatively minor modal groups usually partially or completely separated from the main group. This type is represented by Figures 16(*b*) (Mitimiti, September 1948), 16(*e*) (Otaki, November 1948), and 16(*f*) (Waikanae, 1933 (Hoby 1933)). Dargaville (Figure 16(*c*)) is a somewhat anomalous case, the white figure (January 1950) being of the Wellington type, while the black figure (October 1951) is unique in being the only distribution in which there is some semblance of a balanced population with the strength of the age classes in descending order from left to right. These two widely different distributions might be explained by the lack of sufficiently representative samples covering all parts of the beach. It would appear that Dargaville beach has a peculiar character of its own, distinguished by an extreme variability in size distribution in space and possibly also in time.

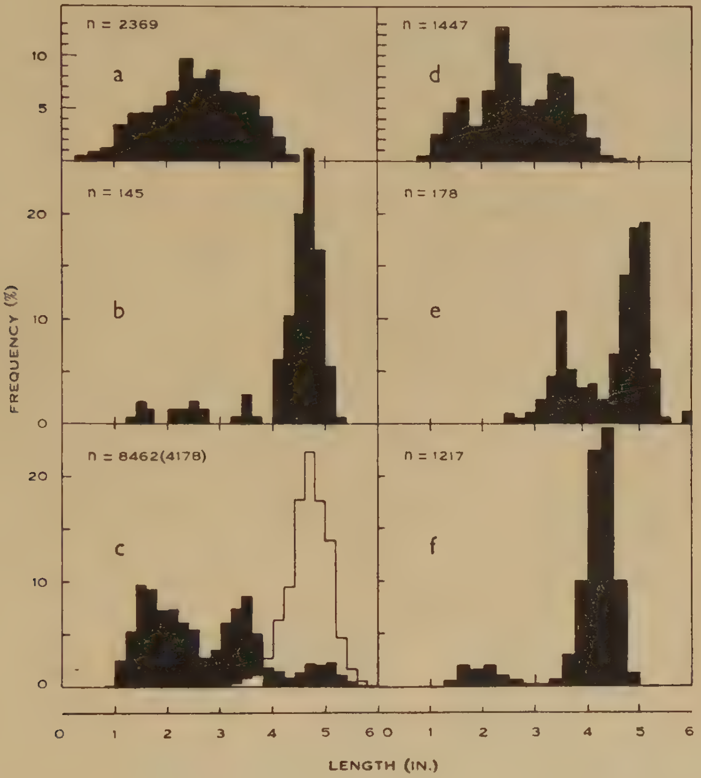

Fig. 16.—Length frequency distributions. *a*, Ninety-mile beach, November 1939 (Rapson 1952); *b*, Mitimiti beach, September 1948; *c*, Dargaville beach, January 1950 (white) and October 1951 (black); *d*, Muriwai beach, October 1939 (Rapson 1952); *e*, Otaki beach, November 1948; *f*, Waikanae beach, 1933 (Hoby 1933).

XI. Zonation of Size Distribution

In the past various observers have noted that toheroa of different sizes may show preferences for different parts of the beach. Rapson (1952, Fig. 2) shows for Glink's Gap, Dargaville beach, a type of stratification which is also discussed in various unpublished accounts by others. The author has not as yet observed such clear segregation of sizes to different levels, but on a few occasions there has been a definite correlation between mean size of toheroa and vertical distribution. Figure 17 shows the length distribution for a traverse taken on Muriwai beach in June 1949, the coefficient of correlation between distance from the upper edge of the bed and size of toheroa being 0.56, which with 680 degrees of freedom (682 toheroas measured) is highly significant.

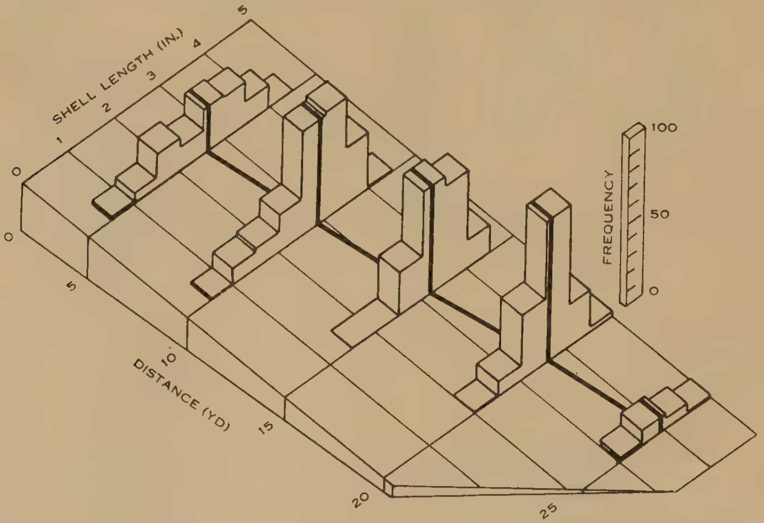

Fig. 17.—Vertical zonation of sizes in transect, Muriwai, June 1949. (Heavy line indicates mean length.) Each histogram shows the size frequency of toheroa for a 2 ft square quadrat dug at 5, 10, 15, etc., yd from the upper edge of the bed.

However, this situation is by no means universal in occurrence, and may even be reversed on some occasions. In the surveys conducted since 1947 it has almost invariably been possible to detect significant differences in the size composition at different levels, but seldom have these differences shown any consistent pattern from bed to bed, or even from transect to transect.

On only one beach has it been possible to detect any definite horizontal zonation of sizes. On Dargaville beach it has been observed by the author and frequently reported by others that distinct "nursery beds" may occur on different parts of the beach. In 1948, for instance, the majority of the smaller toheroa taken were in the neighbourhood of Mahuta Gap, particularly in the beds of the many freshwater streams which dissect the beach.

Here it would seem that some definite physical environmental factor is responsible for the preference, though the perpetually wet sand of the stream bed would appear to be the direct antithesis of the relatively dry areas near high-water mark which have been mentioned by others as the favoured locality for juvenile toheroa.

From the above evidence it appears that physical factors controlling the zonation of sizes are obscure, and that different factors may apply at different times. There is also some indication in the data given in Appendix VI that some form of "contagion" may exist between individuals of similar size.

XII. Evidence for the Presence of Sublittoral Toheroa*

In Section IX it was shown that the age composition of toheroa on both Muriwai and Wellington Province beaches appears to represent an incomplete portion of some larger total population. That other stocks are present besides those sampled on the beach is also suggested very strongly by the comparatively large fluctuations in total numbers which have taken place (Section IV) on certain beaches. In a previous paper (Cassie 1951) it was suggested that the population may be divided into two complementary groups which are defined as the *beach group,* at present the only one which has been observed, and the *sublittoral group.* The hypothesis that the beach group is normally distributed for age does not appear tenable in the light of more recent data, but there is some evidence that toheroa of a certain size (which varies from beach to beach) may particularly favour beach existence. However, before accepting unconditionally the existence of a sublittoral group it is necessary to examine critically all other possible explanations for the phenomena described.

The first is the possibility of a defect in the sampling technique. It has already been shown that unless the estimates of growth rate are grossly in error it is most improbable that any but the first age class could be underestimated in sampling merely because of the smallness of the shells. There does, however, remain the possibility that the zonation of different size classes (Section X) may have resulted at times in beds, particularly of very young toheroa, not being dug at all. This may indeed have been the case in some of the more hastily conducted surveys, but there have been a number of occasions, notably the Muriwai survey of July 1948, in which this contingency was fully appreciated and ample time was available to search exhaustively for "nursery beds". It is also most significant that in the Wellington Province beaches, not once in 21 years has any record been made of more than a few isolated individual toheroa under an inch in length. This is all the more remarkable since at least one worker (Hoby 1933) was investigating the early developmental stages of the species. It must be admitted that there have been instances (on hearsay evidence) of toheroa becoming buried by moving sand up to depths of a foot or more where they might easily escape the digger's fork. However, it seems most improbable that a ciliary feeding mollusc could remain alive for more than very brief periods so buried.

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* The term "sublittoral" is used here in a broad sense to describe the part of the sea bottom below the lowest spring tide level and extending to an unknown (but presumably not very great) depth.

Assuming, then, that the data are valid there remains the question of interpretation. The form of the hypothetical age distribution given in Table 4 and Figures 13 and 15 is dependent largely upon the accuracy of the growth rate determinations for the beaches concerned. While it must be admitted that the growth curves from which these data were derived may have certain deficiencies, they are verified in their general form by Rapson (1952) and Hefford (1928), both of whom reached their conclusions independently of the author. Though discrepancies do exist, they are not of sufficient magnitude to affect the general shape of the age distributions, and indeed the somewhat lower size to age ratio, given by Rapson in some cases, would make the under-representation of the younger toheroa appear even more pronounced. In fact, in order to transform many of the size frequency tables to give a descending series of age frequencies, it would be necessary to postulate a grossly different growth rate. Thus, in the Wellington Province, growth would need to be of the order of 4 in. in the first year but only about 1 in. in the following 10 years. Such a growth curve seems improbable in itself, and even this would not explain the apparent absence at all times of the smaller individuals.

A further alternative exists in the case of Muriwai beach. Other toheroa areas are close at hand, notably Dargaville beach, and it is possible that some interchange may take place between these two beaches, the two together forming a complete and balanced population. It is known that a larger maximum shell size is normally found on Dargaville beach, and that dense beds of juvenile toheroa are frequently reported. Although the mean size distribution of the Dargaville stocks has probably never been satisfactorily determined, there have at times been some indications that the distribution could fill the gaps on either flank of the Muriwai curve. However, such a hypothesis, apart from the difficulty of explaining migration across the mouth of Kaipara Harbour, immediately postulates at least some term of existence in the sublittoral.

However, in the Wellington Province it is hardly conceivable that any such interchange between two beaches with complementary age distributions could be taking place. The same type of distribution (Figs. 14, 16(*c*), and 16(*f*)) has been recorded consistently throughout the Province so that the nearest beach with a different age composition is Muriwai, over 300 miles away.

Thus it does seem almost inevitable that at least some portion of the toheroa population must spend part of its life cycle in the sublittoral region. Unfortunately it has not been possible as yet to make a thorough search for the sublittoral group, but it is hoped that this will be done in the future. Perhaps the outsized shells described in Section VIII (Fig. 6) are derived from toheroa which in their later years have taken up permanent residence offshore, there to grow to a far larger size than is ever reached by their younger relations on the beach.*

The actual mechanism by which the toheroa could migrate from beach to sublittoral region and vice versa can only be inferred. An account which seems to bear some stamp of authenticity is quoted by Mestayer (1921): "At one moment you will see the bare sand as the wave comes in, and immediately it starts to recede, simultaneously and in hundreds of thousands according to the size of the beds, the toheroa emerge from the sand end first, and go down with the receding water, and according to the set of the tide, either up or down the beach. For what distance they go in this way I am unable to say, but certainly they move about. Today you will find a large bed in a certain spot, and a few days afterwards it has quite disappeared." It is quite certain from the author's own observations that some such movements can occur, at least on the beach. On one occasion on Hokio beach about 100 toheroa were marked with a file and allowed to bury themselves, all within an area of about 5 yards square, at low tide. Twenty-four hours later not more than three of these could be found, even though the area had been carefully identified by compass bearings taken on near landmarks. Hoby (1933) also gives some useful contributing evidence suggesting that the toheroa may frequently release itself from the sand when the tide covers the beds. It is shown that on Waikanae beach up to 90 per cent. of the shells are oriented in the sand with their median plane parallel to the coastline, a position which they would automatically assume if, before burying themselves, they had been dropped on their sides by a receding wave, the force of which would almost invariably align the shell with its heavier posterior end pointing seawards. Some weight is given to this conclusion by the fact that this "broadside" position is commoner on days with heavy surf. It would appear then, that the toheroa commonly shifts its position by making use of surf action, rather than by ambulatory movements while buried. It undoubtedly has some ability to move along the beach, as witnessed from time to time by the varying position of beds. For instance, the "winch" bed at Muriwai is defined by a heavy steel ship's capstan which has been a permanent landmark for many years. At times this is surrounded by dense beds of toheroa, while at other times the nearest bed may be as much as half a mile away. On the other hand it is clear that toheroa do not migrate thus on every high tide. Other smaller-scale marking experiments have been more successful in their returns, while the data discussed in Appendix VI also show that some degree of stability may be present at certain times.

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* Mr. A. W. B. Powell says that he believes these shells are of Pleistocene origin. It is hoped that this point will be clarified by the carbon-14 technique.

XIII. CONCLUSIONS

It is now possible to summarize the salient features of the known distribution of the toheroa and the principal factors involved. Table 5 gives what appear to be the principal limiting factors at various levels. The table refers, of course, only to the beach-living toheroa and not to the as yet unknown littoral group of the population.

TABLE 5

LIMITING FACTORS IN DISTRIBUTION OF TOHEROA

Level of Dispersion	Apparent Limiting Factors	Remarks
(1) Geographical distribution	(*a*) Exposed ocean beaches (*b*) Fine sandy substrate (*c*) Sufficient residual moisture to prevent desiccation at low tide (*d*) Abundant phytoplankton	(*a*)-(*d*) must all be present before toheroa will succeed. Temperature and other physical properties of the water are apparently not limiting factors within New Zealand, but the warm temperate zone appears to be the optimum (summer-winter range, 14-20°C)
(2) Vertical zonation	Relative periods of exposure and submergence	Optimum conditions about mean tide level, with upper and lower limits about high- and low-water neap tides. Little variation is apparent in the pattern of the vertical component, but some indication that the distribution may be displaced towards low-tide level in winter and in the colder South Island climate
(3) Horizontal zonation	Residual moisture in sand at low tide	Varies in response to variations in factors such as beach contour or presence of streams. This component is mainly responsible for the apparently contagious distribution
(4) Dispersion of sizes	(*a*) Residual moisture (*b*) Relative periods of exposure and submergence	No constant pattern is evident, but different sizes often show a different response to these factors. There may be a tendency to contagion between animals of like size

Although this table is doubtless not exhaustive in its analysis of the conditions controlling distribution, it does serve to show the critical nature of the natural limiting factors. Since the species has succeeded in finding suitable niches from one end of the New Zealand coastline to the other, and since long stretches of unsuitable coast (which antedate the toheroa geologically) have proved no barrier to dispersal, there seems to be no reason to anticipate that any effort by man to acclimatize it to new beaches is likely to be successful.

It has been shown in previous sections that there are good reasons for believing that the toheroa beds found in the intertidal zone on exposed beaches do not constitute the whole, or even necessarily a very large part, of the total population. This conclusion may affect the management of the toheroa as a potential food resource in two ways.

In the first place, it indicates that the pressure of exploitation, whether commercial or private, may not have so serious an effect on the total population as was previously believed. The presence of a reserve stock which is protected absolutely from present methods of exploitation must reduce to some extent the likelihood of the spawning stock being depleted below the level required to maintain recruitment. Since the younger toheroa in particular appear to be largely immune from disturbance (especially in the Wellington Province), utilization will tend to be directed toward the older year-classes which are likely to give a greater yield of edible meat.

On the other hand, we are still further removed from an accurate quantitative estimate of the number of toheroa which may safely be harvested for human consumption.* If the sublittoral toheroa occurs in relatively large numbers, spawns regularly, and interchanges freely with the beach group, the necessity for control of exploitation on the beach will be very much reduced, if not removed altogether, though offshore dredging operations, if they ever came into operation, might present a serious conservation problem. Nevertheless, whatever the condition of the sublittoral stock, it seems unlikely that any control of the numbers which present themselves on the beach will ever be possible. In certain localities the numbers may be so small that the entire standing crop could conceivably be removed by intensive digging. If spawning were restricted to the beach stock, it would be undesirable to allow such a situation to prevail for any length of time.

Thus, before a complete understanding can be gained of the toheroa and of the most appropriate means of exploiting it, several further questions will need to be answered: How large is the sublittoral group and where is it located? How often does interchange between the two groups take place, and what factors influence these movements? Are toheroa capable of spawning in the sublittoral or must they proceed inshore for this purpose?

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* Rapson (1954, Table 7) gives estimates of "optimum population" and "production of meats" for four beaches, but does not give any indication of how these were computed. It would seem that at least some of the data are inadequate for the purpose for which they have been used, e.g. it is doubtful whether 15 samples from Muriwai beach give a true picture of the availability of phytoplankton or of its utilization by toheroa.

XIV. ACKNOWLEDGMENTS

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APPENDIX I

Canned Toheroa Production

Table 6 is a summary, taken from Annual Reports of the New Zealand Marine Department, of the production and exports of canned toheroa. Total production statistics are missing for recent years since only one cannery has been in operation and production of individual factories is not published. The actual numbers of toheroa represented can only be estimated approximately. When whole toheroa are canned the average is about 12 to a 1-lb tin, but for soup this number would probably be halved. Unfortunately there are no records available of the relative quantities of the two products packed, though it is known that no soup has been produced since 1947. Hefford estimated that in 1940 (probably the peak production year) about 1½ million toheroa were canned.

TABLE 6

CANNED TOHEROA PRODUCTION AND EXPORTS, 1928-1954

Data from Annual Reports of Marine Department

Year	Total (100 lb)	Exports (100 lb)	Total Value (£100)	Year	Total (100 lb)	Exports (100 lb)	Total Value (£100)
1928	74	—	53	1942	—	151	12*
1929	240	—	124	1943	1038	95	45
1930	840	462	42	1944	1071	128	65
1931	288	133	24	1945	857	158	50
1932	Nil	Nil	Nil	1946	690	51	46
1933	520	193	28	1947	434	141	29
1934	620	247	58	1948	266	64	22
1935	723	248	31	1949	—	311	32*
1936	105	330	63	1950	—	357	37*
1937	486	472	48	1951	—	289	30*
1938	696	423	37	1952	—	424	48*
1939	850	632	52	1953	—	64	5*
1940	1696	876	101	1954	—	180	22*
1941	—	745	53*				

* Export value only.

APPENDIX II

Statistical Aspects of Spatial Distribution

It has already been noted in Section VII that the distribution of toheroa on the beach is far from random. Figure 18 illustrates the frequency of sample counts for quadrats (*a*) and beds (*b*) for Muriwai, July 1948. In both cases the greatest number of counts occur toward the zero end of the scale, and the general form of the distribution suggests a highly over-dispersed or aggregated condition. This is further demonstrated by the fact that the variance is considerably greater than the mean of sample counts, whereas in a Poisson (or random) distribution these two parameters would be approximately equal. When mean quadrat count for each bed is plotted against the standard deviation the points fall approximately on a straight line passing through the origin, suggesting that the distribution is similar to the negative binomial series for which the variance, σ^2, is given by the equation:

$$\sigma^2 = m + m^2/k$$

where m is the mean and k is a constant.

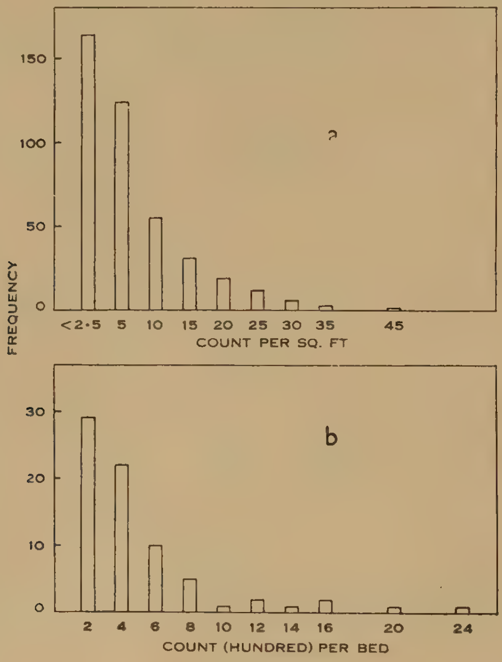

Fig. 18.—Spatial distribution in sample counts, Muriwai, July 1948. *a*, frequency of counts per sq. ft quadrat; *b*, frequency of counts per bed.

The nature of the distribution reflects in several ways on the technique which will be most appropriate for sampling the population. In the first place, although the systematic process which has been adopted in these surveys will give an unbiased estimate of the total population number, it can give no valid estimate of the sampling error. To obtain some idea of the magnitude of this error, the quadrat counts for Muriwai, July 1948, were stratified by taking the sum of every 16th sample, thereby obtaining

16 different estimates of the sampling mean. The coefficient of variation of the mean of these estimates was found to be 3.71 per cent. In some of the less intensive surveys this value would be very much higher, as much as 30 per cent. in some cases. The coefficient of variation is appropriate only to the sampling data and is not necessarily an unbiased estimate for the population. It does, however, give some idea of the order of magnitude of the sampling error of population estimates and suggests that in Table 1, for instance, the only apparent fluctuation in total population which is significant is the 1937-38 drop from 15 to less than 1 million. Thus, unless extremely intensive and laborious sampling is undertaken, sampling errors are likely to be of considerable magnitude, and in future it will be advantageous to employ a random sampling technique so that sampling error may be estimated and reduced within suitable limits to demonstrate fluctuations in total population.

A second feature brought out by Figure 18 is that the commonest sample count is at the zero extremity of the distribution, while the more densely populated sampling areas which are most likely to influence the estimated mean will tend to be under-represented. For instance, if only half the beds were estimated, there would be an even chance that the largest bed, containing about 0.76 million toheroa, would be omitted. This would contribute a considerable error to the mean estimate for 76 beds, which is only 0.14 million. Thus for maximum efficiency it is desirable that sampling should be stratified in such a way that the entire range of the toheroa on any one beach is covered as comprehensively as possible.

The need for comprehensive sampling does not necessarily imply an increased sampling intensity, but rather that a large number of small samples will be preferable to a small number of large samples. The small sample is in itself an advantage since, as will be seen from the equation above, variance will increase as the square of the mean (provided k is small and m is greater than unity, both of which conditions are fulfilled in this case). Under such conditions the smaller sample has a decided advantage in that it introduces no greater a sampling error and permits time and energy to be diverted to taking more samples. There is, however, a certain practical limit beyond which sample size cannot be reduced without introducing bias. This is determined by the uncertainty in deciding whether a toheroa near the margin of a quadrat should be counted or not. The smaller the sampling unit the greater the number of individuals in this marginal zone and the greater the tendency toward a biased sample. If we accept 10 per cent. as the maximum permissible number of marginal individuals, and 1 in. as the minimum range within which the position of an individual can be determined, the smallest sample size which can be employed will be a circle of 10 in. radius. The 2 ft square quadrat is fairly close to this minimum, but the 15 × 7/12 ft section of transect does not fulfil the conditions so well since, while the area has been doubled, the length of the margin has been nearly quadrupled.

It is possible, however, to make use of a biased sample, provided the bias is constant and can be estimated. It might then be possible to reduce the sampling unit even to the extent of eliminating digging altogether and employing a spear, each probe of the spear constituting a sample. It will be noted that in such a case the effective sampling area would be equal to the mean cross-sectional area of a toheroa and that no sample could contain more than one individual. Such a method, if suitably calibrated against unbiased samples, would be effective provided that dead shells or stones were absent or could be distinguished from live toheroa.

A further feature of spatial distribution on the beach is seen in the relationship between traverse and quadrat counts. It was found for the Muriwai (July 1948) survey that there was a correlation of 0.874 between the traverse counts and the counts for the central quadrats of the same traverses. Since there were 175 traverses, giving 173 degrees of freedom, the correlation is highly significant. It was also suspected that the traverse count might be related to the number of quadrats (or in effect to the width of the bed). For a series of 32 traverses from the same survey it was found that the traverse counts had a correlation of 0.926 ($P < 0.001$) with the central quadrat counts, 0.416 ($P = 0.2$) with the number of quadrats, and a multiple correlation of 0.945 ($P < 0.001$) with the two combined. Thus the contribution made by bed width to the estimate of the numerical strength of the traverse is relatively slight, compared with that of the central quadrat. This is not altogether surprising, since vertical zonation would appear to be controlled largely by the relative times of exposure and submergence by the tide. Provided the slope of the beach remains uniform, the relative density of toheroa will retain the same vertical pattern, even though the absolute density fluctuates with horizontal variation in other factors. Changes in beach slope will tend to vary the spread of this pattern by altering the horizontal component of tidal rise and fall. It would appear that such variations in gradient do occur but are small and do not have a great effect on pattern spread. Although no appropriate quantitative data on beach contour are available it was evident on the flatter northern section of Muriwai beach that beds were appreciably wider, and the central quadrats contained a smaller proportion of the total traverse count. This relationship suggests a further method of increasing sampling efficiency. From the correlation coefficient (0.874) it will be seen that 76 per cent. (0.874^2) as much information regarding relative abundance over the whole beach could be achieved from one sample taken at the centre of each traverse. Since there is an average of nearly four quadrats to each traverse, an appreciable saving in effort would result from a judicious blending of traverse and central quadrat sampling.

APPENDIX III

Length-age Relationship

Some of the information from which Figures 11-14 were constructed is summarized in Tables 7-9. Certain points have been omitted from the graphs, either because they are very close in value to others already plotted, or because there is some doubt as to the validity of the dissection. All such omissions are indicated in the tables by bracketing the appropriate

TABLE 7

LENGTH-AGE RELATIONSHIP, MURIWAI (FIG. 11)

Bracketed values indicate omission of points from graph (see text); asterisks indicate that the estimated mean is doubtful

(*a*) *July* 1948

Age (yr)	Shell Ages			Length Frequency Ages		
	n	$\bar{x}$	s	n	$\bar{x}$	s
0+	—	—	—	740	1.55	0.25
1+	(8)	(2.35)	(0.28)	3976	2.36	0.29
2+	39	3.10	0.22	—	—	—
3+	57	3.78	0.23	—	—	—
4+	49	4.10	0.22	—	—	—
5+	12	4.54	0.15	—	—	—
6+	(1)	(4.6)*	—	—	—	—
7+	—	—	—	—	—	—
8+	(1)	(4.7)*	—	—	—	—

(*b*) *Miscellaneous Length Frequency Ages*

Date	0+ Age Class			1+ Age Class			2+ Age Class		
	n	$\bar{x}$	s	n	$\bar{x}$	s	n	$\bar{x}$	s
Oct. 1939	295	1.48	0.25	620	2.43	0.25			
Aug. 1947	112	1.43	0.24	(839)	(2.41)	(0.30)			
Dec. 1948	—	—	—	126	1.85	0.30	317	2.84	0.25
June 1949	233	1.72	0.25	75	2.18	0.21			
Feb. 1950	(77)	(0.70)*	(0.30)	294	1.62	0.24			
Nov. 1951	265	1.57	0.25	—	—	—			
Aug. 1952	195	1.53		5529	2.22				
Dec. 1953	—	—	—	25	1.74	0.20	50	2.62	0.21

values, while cases where the estimated mean is doubtful are indicated by an asterisk. It should be noted, however, that the majority of values so

TABLE 8

LENGTH-AGE RELATIONSHIP, DARGAVILLE (FIG. 13)

Bracketed values indicate omission of points from graph (see text); asterisks indicate that the estimated mean is doubtful

(*a*) *September* 1948

Age (yr)	Shell Ages			Length Frequency Ages		
	n	$\bar{x}$	s	n	$\bar{x}$	s
0+	8	1.79	0.16	8	1.27	0.16
1+	6	2.55	0.12	92	2.04	0.29
2+	82	2.84	0.17	260	2.92	0.25
3+	15	3.63	0.14	(640)	(3.67)	(0.23)
4+	22	4.02	0.14	—	—	—
5+	54	4.37	0.16	—	—	—

(*b*) *Shell Readings, September* 1948

Age (yr)	n	$\bar{x}$	s
1	32	1.84	0.16
2	32	2.58	0.17
3	32	3.19	0.16
4	32	3.70	0.19
5	32	4.13	0.18
6	32	4.47	0.19
7	32	4.68	0.18
8	29	4.82	0.20
9	20	4.94	0.20
10	11	5.07	0.20
11	(6)	(5.15)*	(0.20)
12	(2)	(5.4)*	(0.2)
13	(1)	(5.3)*	(—)

(*c*) *Length Frequency Ages, October* 1951

Age (yr)	n	$\bar{x}$	s
0+	1573	1.66	0.34
1+	662	2.28	0.23
2+	780	3.34	0.29

(*d*) *Length Frequency Ages, November* 1938

Age (yr)	n	$\bar{x}$	s
0+	941	1.63	0.25
1+	(565)	(2.45)*	(0.25)
2+	(1474)	(3.40)*	(0.33)

marked are not inconsistent with the other points. The following symbols are used in Tables 7-9:

n = number of shells measured,
$\bar{x}$ = mean shell length (in.),
s = standard deviation of shell length (in.).

TABLE 9

LENGTH-AGE RELATIONSHIP, WELLINGTON PROVINCE (FIG. 14)
Bracketed values indicate omission of points from graph (see text); asterisk indicates that the estimated mean is doubtful

Locality	Date	Length Frequency Ages		
		n	$\bar{x}$	s
Waikanae	Apr. 1933	23	1.72	0.20
	May 1933	16	1.81	0.21
	June 1933	30	1.91	0.25
	Oct. 1933	15	2.49	0.21
Waitarere	Jan. 1938	48	0.29	0.08
	Mar. 1938	5	2.48	0.22
	Oct. 1940	25	2.04	0.38
Hokio	June 1948	40	2.87	0.28
	Nov. 1948	55	3.27	0.32
Waikawa	Nov. 1948	(53)	(3.52)*	0.36

APPENDIX IV

Dissection of Length Frequency Data into Age Classes: Goodness of Fit

The dissection of toheroa length frequency data into apparent age classes by the probability paper technique has been referred to in Section VIII and a graphical example of such an analysis given in Figure 17. The numerical information relating to this figure is presented in Table 10. Column l gives the lower class mark in 0.1-in. intervals, while f is the observed frequency of toheroa of each size in the sample. The three columns $\mathbf{f}_0$, $\mathbf{f}_1$, and $\mathbf{f}_2$ are the expected frequencies in the 0+, 1+, and 2+ age classes respectively, and have been computed from the parameters n (number of toheroa), $\bar{x}$ (mean length), and s (standard deviation of length), using a table of the ordinates of the normal distribution. The sums of these three sets of frequencies give the values **f**, which describe the continuous curve in Figure 17. Finally, χ^2 gives a test of goodness of fit, with degrees of freedom equal to the number of classes, less one for each parameter (i.e. three for each age class). The χ^2 test has not been applied beyond 3.4 in. since the observed frequencies from this point onward come under the influence of the flank of the fourth (3+) age class.

The probability paper technique may be subject to criticism on the grounds that it makes an unwarranted assumption, viz. that measurement data from homogeneous naturally occurring populations are normally distributed. For this reason, care has been taken in this work to place reliance only on those sets of sample parameters where a distinct mode occurs. It has been found in nearly every such case that the distribution so obtained approximates very closely to normal. It is of course not possible to establish an exact criterion for a "distinct mode", and borderline cases (e.g. the 2+ age class in Table 11) have been disregarded in the evaluation of growth rate, though in some instances they have been recorded and marked with an asterisk in Tables 8-10. Thus the principal function of the probability paper technique is not to distinguish components which would not be evident in a simple length frequency table or histogram, but to evaluate more precisely and expeditiously those components which are already apparent, by taking into account not only the modes but the whole range of variation.

TABLE 10

DISSECTION OF LENGTH FREQUENCY DATA INTO AGE CLASSES

Sample taken between 14.0 and 14.5 miles north of beach entrance, Muriwai beach, December 1948

l*	f	f_0	f_1	f_2	f	χ^2
1.3	—	0.3			0.3	0.013
1.4	1	0.8			0.8	
1.5	2	1.9			1.9	
1.6	4	3.7			3.7	
1.7	6	4.8			4.8	0.300
1.8	3	4.9			4.9	0.737
1.9	5	4.0			4.0	0.006
2.0	1	2.2			2.2	
2.1	2	0.9	0.1		1.0	0.001
2.2	—	0.4	0.5		0.9	
2.3	1	0.1	1.6		1.7	
2.4	5		4.5		4.5	
2.5	9		9.0		9.0	0.000
2.6	13		12.3	0.2	12.5	0.020
2.7	10		12.3	0.5	12.8	0.612
2.8	11		9.0	1.8	10.8	0.004
2.9	10		4.5	4.5	9.0	0.111
3.0	15		1.6	9.9	11.5	1.065
3.1	15		0.5	18.4	18.9	0.805
3.2	21		0.1	25.6	25.7	0.860
3.3	27			29.3	29.3	0.181
3.4	27			28.3	28.3	0.060
	188	24.0	56.0	118.5	198.5	4.775
3.5	29			20.3	20.3	—
3.6	22			12.5	12.5	—
3.7	34			5.6	5.6	—
3.8	22			2.2	2.2	—
3.9	29			0.7	0.7	—
4.0+	209			0.2	0.2	—
n	533	24.0	56.0	160.0	240.0	
x		1.81	2.70	3.36		
s		0.19	0.18	0.22		

Total χ^2 (1.3 to 3.4 in.) $= 4.775$; $P > 0.5$ (d.f. $= 15 - 9 = 6$)

* Lower limit of 0.1-in. class. Mid point of class $= l + 0.05$ in.

APPENDIX V

A Replicate Sampling Experiment

The following experiment conducted on Muriwai beach in June 1949 was originally designed to test the consistency of the sampling technique, but some light is also cast on several other questions. Two routine traverses were redug at one end of a bed which had been sampled 2 days previously. The positions of traverses and quadrats were approximately the same as on the previous day, though no particular precautions were taken to make them identical. Table 11 shows the χ^2 test applied to the results.

The results have been pooled in two ways: between traverses, within size groups (columns); and between size groups, within traverses (rows). In each case total χ^2 indicates in effect the relation between absolute frequencies, pooled χ^2 that between totals, and interaction (total minus pooled) χ^2 that between relative frequencies. It will be seen that some of the values are significant at the 5 per cent. level, but none at the 1 per cent. level. This suggests that there has been some significant change in the populations sampled, but that the change has not been great enough to mask the general similarity both in size composition and numbers between the two days. In traverse 1 the high values of P (total) and P (interaction) and the lower value of P (pooled) show that while the change in total numbers verges on significance, the size composition is virtually unchanged. In traverse 2 on the other hand, absolute size distribution has changed significantly but total numbers and relative size distribution, though they have varied appreciably, do not quite reach the 5 per cent. significance level. The totals for the two traverses combined give (as might be expected) low probabilities comparable to those in the more densely populated traverse 2, though significance is only reached in the pooled χ^2. Pooling frequencies between the two traverses gives slightly higher probabilities throughout, owing to the tendency for certain discrepancies to cancel out. The interaction column suggests that, while the overall relative size composition has not changed appreciably ($P = 0.7$) there is a significant difference ($P = 0.01$) between the two days in absolute numbers of toheroa. Bearing in mind the tendency to over-dispersion already noted, plus the fact that the traverses may have changed a little in position, it would seem that the distributions on the two days show a striking similarity. Since it is most improbable that any large-scale movement of individuals could take place without disturbing this similarity, it is reasonable to assume that the majority of toheroa have remained stationary or very nearly so. This is in marked contrast to the apparent migratory tendencies (Section XI) observed on another occasion with marked toheroa.

A further point of interest is found by examining the source of the high value of χ^2 (total = 39.308) in traverse 2. From Table 11(a) it is

TABLE 11

REPLICATE SAMPLES, MURIWAI, 14.5 MILES NORTH OF ENTRANCE, 1949

(a) Raw Data and Individual Test of Significance

(l)*	Traverse 1			Traverse 2		
	June 24	June 26	χ^2	June 24	June 26	χ^2
1.2				1		1.000
1.3				—		
1.4				—		
1.5				—		
1.6				—		
1.7				2		
1.8				1		
1.9				2	3	
2.0				—	3	1.923
2.1	1		2.000	—	3	
2.2	1			4	3	
2.3	1	2		*3*	—	*4.571*†
2.4	1	—		*3*	—	
2.5	—	—		*5*	*3*	
2.6	1	—		8	2	3.600
2.7	1	—		*1*	*7*	*4.500*
2.8	1	2	0.200	9	7	0.250
2.9	2	—		9	13	0.727
3.0	—	—		*12*	*26*	*5.158*
3.1	1	—	1.000	13	20	1.485
3.2	2	2		17	23	0.900
3.3	3	1		16	14	0.133
3.4	3	1	2.000	24	33	1.421
3.5	3	1		27	42	3.261
3.6	—	2	0.143	35	30	0.385
3.7	3	2		34	29	0.397
3.8	5	1	2.778	33	42	1.080
3.9	2	1		37	40	0.169
4.0	*12*	*3*	*5.400*	56	55	0.091
4.1	5	7	0.333	23	47	2.800
4.2	4	5	0.111	*46*	*29*	*3.853*
4.3	6	6	0.000	26	30	0.285
4.4	4	5	0.111	18	15	0.273
4.5	1	3	0.000	8	11	0.474
4.6	2	—		6	8	0.286
4.7	—	1	0.200	6	8	0.286
4.8	2	1		2	1	0.000
4.9	—			1	2	
5.0	1			—	1	
5.1				1	1	
5.2				1		
	68	46	14.276	490	551	39.308

* Lower limit of 0.1-in. class. Mid point of class $= l + 0.05$ in.

† Italics indicate $P < 0.05$.

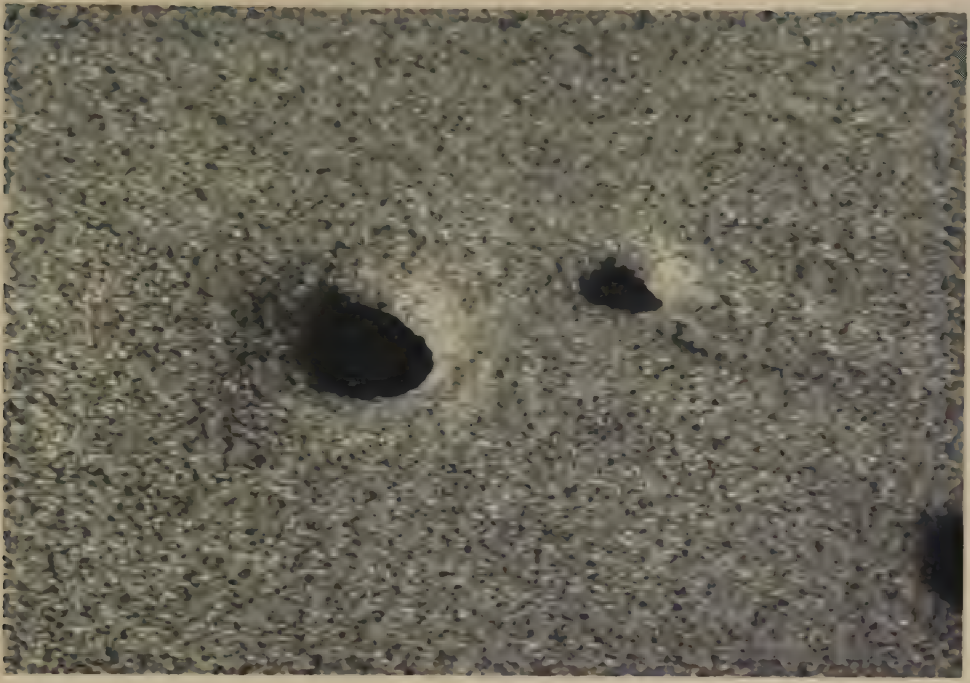

Fig. 1.—The two siphon holes indicating the presence of a toheroa in the sand.

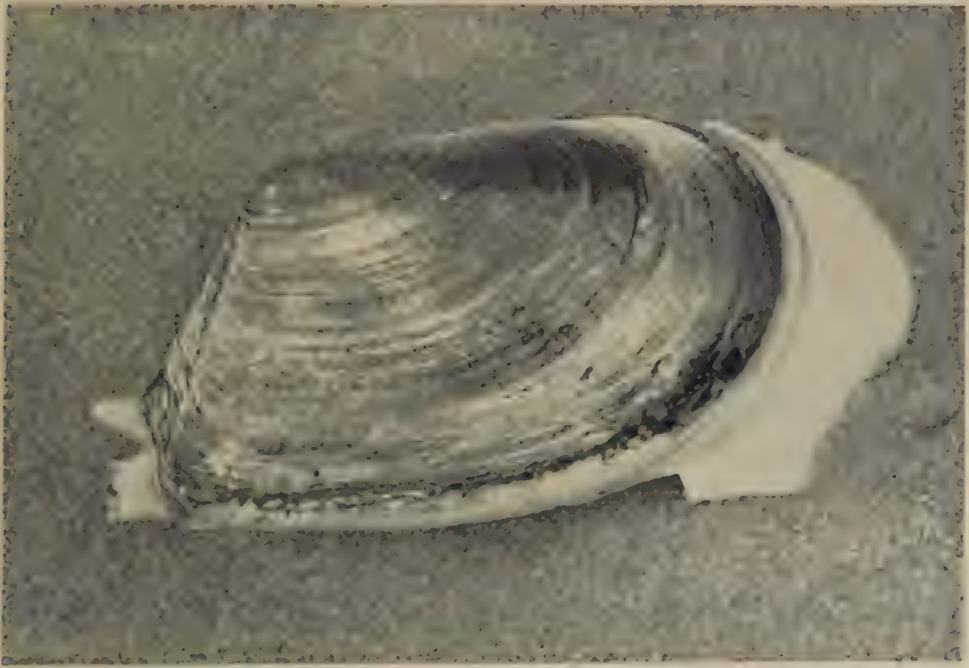

Fig. 2.—A toheroa left lying on the beach commences to rebury itself.

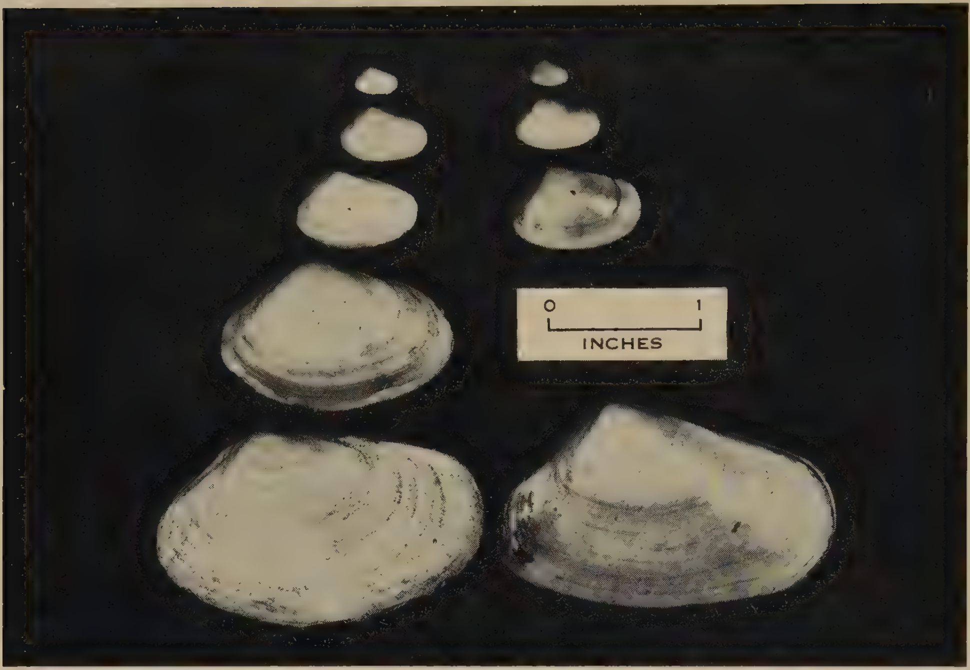

Fig. 1.—Comparison of the external features of the toheroa (*Amphidesma ventricosum*) (left) and tuatua, *A. subtriangulatum* (right).

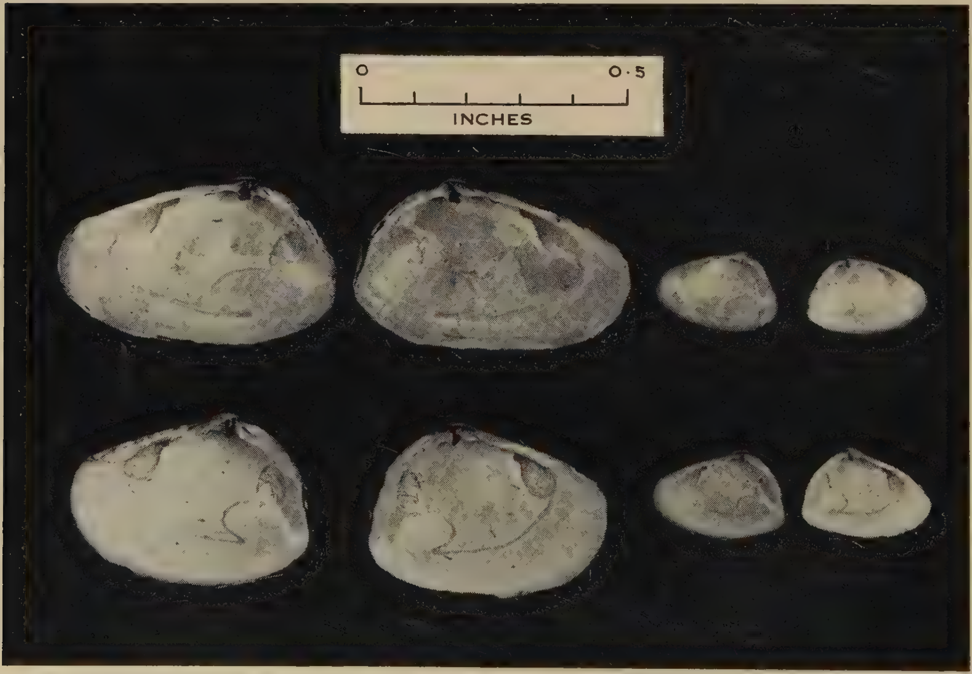

Fig. 2.—Comparison of the internal shell features of *A. ventricosum* (upper) and *A. subtriangulatum* (lower).

TABLE 11 (*Continued*)

(*b*) *Detailed Test of Significance*

	Traverse 1			Traverse 2			Total		
	χ^2*	D.F.†	P‡	χ^2	D.F.	P	χ^2	D.F.	P
Total	14.276	13	0.3	39.308	26	0.02	53.584	39	0.05
Pooled	4.246	1	0.05	3.574	1	0.05	7.820	2	0.02
Interaction	10.030	12	0.5	35.734	25	0.05	45.764	37	0.05

	Pooled			Interaction		
	χ^2	D.F.	P	χ^2	D.F.	P
Total	40.647	29	0.1	12.937	10	0.2
Pooled	1.317	1	0.2	6.503	1	0.01
Interaction	39.330	28	0.1	6.434	9	0.7

* $\chi^2 = (f_1 - f_2)^2/(f_1 + f_2)$.

† Number of degrees of freedom.

‡ Probability of a higher value of χ^2 in random sampling.

seen that nearly half of this total is contributed by four individual size groups (italics). If these are subtracted from the total:

$$\chi^2 = 21.226, \quad \text{d.f.} = 22, \quad P = 0.5.$$

This suggests that local clusters have formed of toheroa all of similar size, indicating a possible contagion not only between individuals, but also between individuals of like size, a phenomenon to which reference has been made in Section XI. This type of contagious distribution is frequently noted in fish, but it is interesting to note the possibility of its also occurring in a mollusc species.

UNDERWATER STUDIES ON THE TASMANIAN COMMERCIAL SCALLOP, *NOTOVOLA MERIDIONALIS* (TATE) (LAMELLIBRANCHIATA: PECTINIDAE)

By A. M. Olsen*

(*Manuscript received March* 10, 1955)

Summary

Population densities of scallops in the D'Entrecasteaux Channel (Tas.) fishing areas have been assessed by diving. In shelving positions the scallops occur in greatest densities between 4 to 8 fm, and on flat areas within these limits they may be found everywhere, but in varying concentrations. The so-called "strips" or "beds" of commercial fishermen are merely higher-density aggregations. The most extensive bed, 1 sq. mile in area and averaging six scallops/sq. yd, contained about 18 million scallops.

Two scallops/sq. yd is considered the minimum economic limit for operation provided the meat yield (roe included) per 1000 scallops is not less than 33 lb.

The successful spatfall and subsequent development of a strong year class is very sporadic and, as yet, unpredictable. In 1954, the 1948 year class scallops entered the fishery, which until then had been almost entirely dependent on the scallops spawned about 1940.

Water movements, particularly tidal currents, have a marked influence on the distribution of the spat. In areas of strong tides the long axes of areas of high concentrations run lengthwise to the flow whereas in areas of slow movement the distribution is even, whilst eddy systems appear to concentrate the spat.

Concentrations of 30-36 scallops/sq. yd were reduced in 4 years by starfish to five/sq. yd, i.e. a 75-80 per cent. mortality occurred.

During the course of this underwater investigation the individuals of a selected bed were observed to make random movements, yet the known location of a bed did not change.

I. Introduction

Much of the earlier published work on scallops, reviewed by Dakin (1909) and Gutsell (1930), was concerned with morphological, anatomical, and histological studies; whereas in recent years increased attention has been paid to the study of scallops in their natural environment. Attempts have been made to determine the population densities of known scallop beds by dredging for fixed time periods. By this method Dickie (1953) found that the maximum concentration on the Digby (Canada) beds was about two scallops/sq. yd. Working with a 6-ft dredge on the English Channel beds, Baird (1952) assessed the concentrations by the number of scallops per 15-min haul and expressed his results by stating whether the beds were satisfactory or otherwise for commercial exploitation.

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In Mutsu Bay (Japan) Yamamoto (1952), using a bottom sampler, found juvenile scallop concentrations up to 250/sq. m, and later he transplanted large numbers of these scallops and followed their effect by the changes produced in the benthic communities on the man-made beds (Yamamoto 1951). He found that after the initial shock phase there was virtually no difference between the natural and the artificial scallop beds.

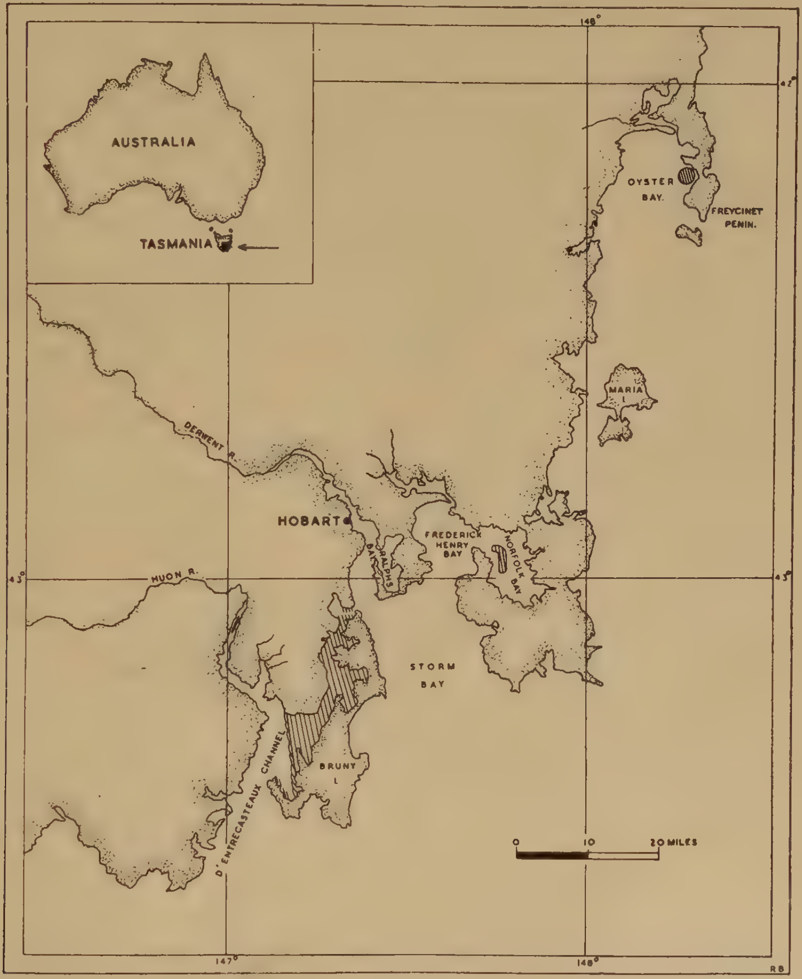
148°
42°
AUSTRALIA
TASMANIA
OYSTER BAY.
FREYCINET PENIN.
MARIA I.
DERWENT R.
HOBART
FREDERICK HENRY BAY
RALPHS BAY
NORFOLK BAY
43°
HUON R.
STORM BAY
BRUNY I.
D'ENTRECASTEAUX CHANNEL
0 10 20 MILES
147°
148°
RB

Fig. 1.—Scallop areas in south-eastern Tasmania (indicated by hatching).

In all these studies indirect methods of assessment have been used, whereas results reported in this paper were obtained by direct visual observation. So far as the writer is aware, this is the first report of a comprehensive long-term underwater study of scallops.

This investigation was undertaken to obtain direct visual evidence about, and a better understanding of, the ecology of Tasmanian scallops, in particular the commercial scallop, *Notovola meridionalis* (Tate). In the industry there are many conflicting theories about the distribution, concentration, and behaviour of scallops with dredging.

During 1947 three separate series of descents at about 3-monthly intervals were made in the D'Entrecasteaux Channel (Fig. 1) to ascertain whether scallops were subject to seasonal migration and behaviour. The examinations were all carried out on well-known scallop beds and descents down to 10 fm were made from the parent vessel anchored over selected sites.

On the bottom systematic sweeps were carried out by the writer and a professional diver, who on their return to the surface, were immediately questioned, out of earshot of each other, about their observations below. Their answers were written down on a prepared detailed questionnaire designed for full extraction of the available information. At the end of each day's work the results were tabulated and compared. Using this method little conflict between the two sets of observations was found. Where any disagreement did occur each diver before descending was given specific instructions to watch carefully for the matter in dispute so that it could be settled.

From 1951 to 1954, annual examinations lasting from at least a week up to a fortnight were made each summer, whilst in the winter of 1951 a week's survey was also carried out during the 3-month open season for scallops. A total of 49 hr was spent on the bottom during the course of this investigation.

Improvements in the equipment and the introduction of two-way telephone communication in 1951 had enabled the scope of the investigation to be widened to include size and population densities of the various scallop beds. This information was obtained by drifting at a known rate over the scallop beds while the diver relayed his observations to a recorder on the diving vessel (Olsen 1953). Because the rate and direction of drift were known and the concentration of scallops had been recorded, it was possible to calculate the length, width, and population density of scallop beds.

II. Equipment and Methods

The standard full-dress diving gear and pumps (British Admiralty 1943) manufactured by Siebe, Gorman & Co. Ltd., England, were used throughout.

In 1951 the pumping equipment was fully mechanized when a B.E.N. type A4 compressor rated to supply 15 cu. ft air/min at 350 r.p.m., rising to 29 cu. ft/min at 650 r.p.m., was installed. The compressed air was stored in a large cylindrical tank (6 ft long and of 3-ft dia.) capable of withstanding pressures up to 100 lb/sq. in. Its calculated capacity was approximately 43 cu. ft, sufficient for two divers for 15 min at 40 ft assuming that each diver required 1½ cu. ft of air/min.

A further improvement was the installation of a 12-V two-way telephone complete with amplifying equipment (Guided Radio Corporation, New York, No. 653) for use between diver and surface.

Underwater measurements were made with a marked 3-ft length of rolled steel electrical conduit fitted at one end with a 4-in. dia. cork float. The concentrations were estimated in numbers per sq. yd as the mean of a series of counts of the number of scallops in a square with 3-ft side.

A simple device made from a piece of 3 by 2 in. weighted hardwood 3 ft long, secured in the centre by a line from the diving vessel, served as a seat for the divers, who were towed along the sea floor. They buoyed themselves so as to float just clear of the bottom. A lanyard looped around the base of the helmet and tied to the seat rope left the diver's hands free. This simple seating arrangement eliminated the fatigue of walking considerable distances under water.

The rate of drift over the bottom was measured by the diver, who counted the number of his boot lengths placed heel to toe in a given time.

III. The Environment

The location of the scallop beds and hydrological conditions in the D'Entrecasteaux Channel have been described previously (Fairbridge 1953). A brief description of the bottom configuration of the channel is given because of the influence which the configuration has on the distribution of scallops.

The Channel (Admiralty Chart No. 960) is located in an area where the whole of the coastline formerly above sea-level has been inundated.

The 25 mile long Channel (Fig. 2) is roughly divisible into: (i) a deep, open southern entrance (22 fm); (ii) an extensive, relatively shallow mid-section (7 fm); (iii) a narrow, deeper northern channel. The southern section is the old bed of the Huon River, the present junction of which is about 5 miles above the Channel entrance. There is a steep rise out of the 22-fm channel to the 10 mile long and 7 fm deep mid-section, which narrows and deepens towards its northern end.

Whereas the southern section has a relatively constant depth, the 25-fm northern trough ends abruptly against a 7-fm submarine ridge across the northern entrance. The shallower area represents a sunken saddle in the low range of coastal dolerite and mudstone hills which continue southwards as the steep eastern shore of Bruny Island. Except for the Dennes Point beach inside the entrance, the sides of the northern channel are steep and drop sharply into 2-3 fm before giving way to sand which continues out into 6-9 fm. With increasing depth the silt content rises, and over 10 fm the bottom is mostly oozy mud. Almost similar conditions prevail in the southern section, where the narrow beaches shelve sharply through sand to thick mud.

In the mid-section (the main scallop beds) there exists a variety of bottom conditions. In general there is fine sand at each end of an area of coarse sand and fine shell located between Gordon and Middleton. Below Gordon the fine sand covers all the bottom out to about 10 fm (Fig. 2).

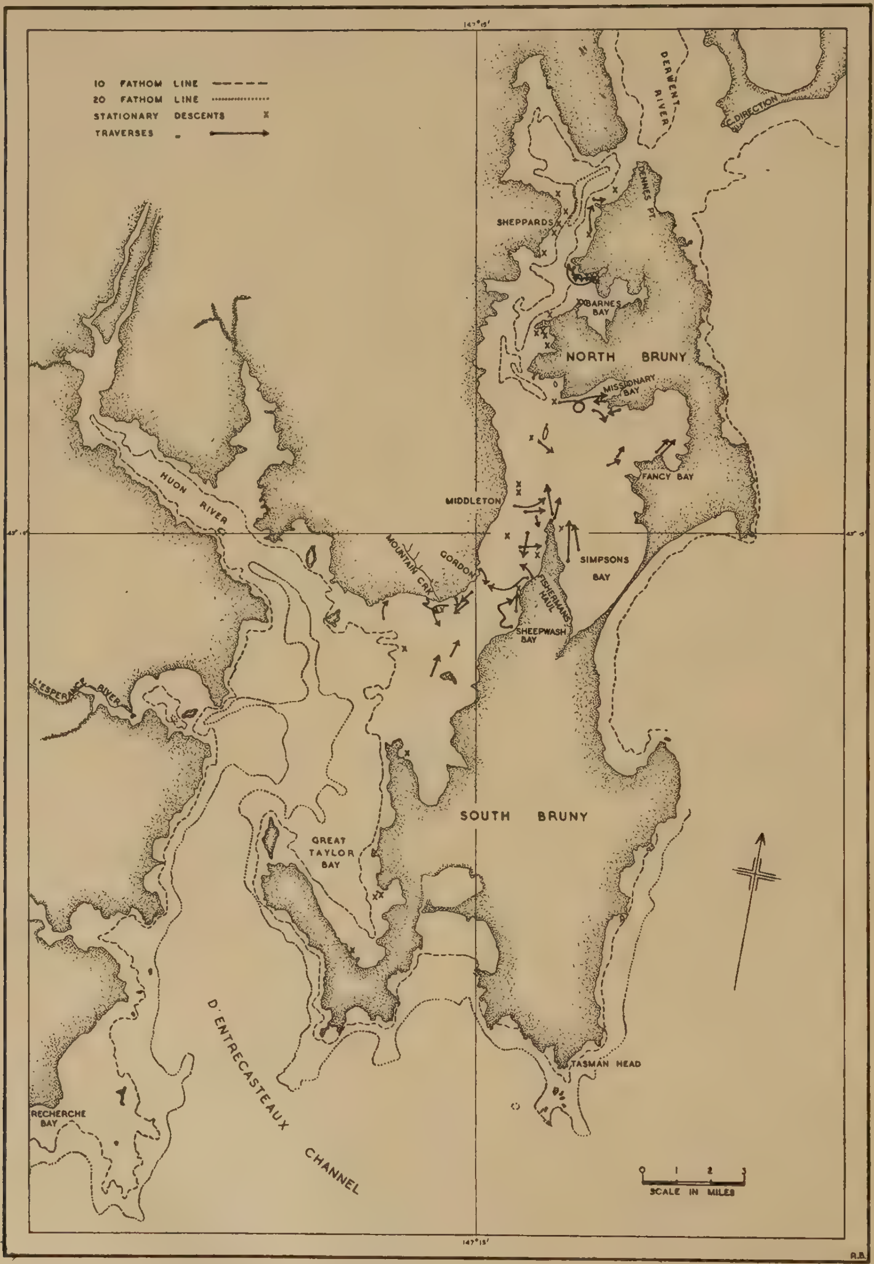
10 FATHOM LINE
20 FATHOM LINE
STATIONARY DESCENTS x
TRAVERSES
147°15'
DERWENT RIVER
C. DIRECTION
DENNES PT.
SHEPPARDS
BARNES BAY
NORTH BRUNY
MISSIONARY BAY
FANCY BAY
MIDDLETON
HUON RIVER
MOUNTAIN CRK
GORDON
SIMPSONS BAY
FISHERMANS HAUL
SHEEPWASH BAY
L'ESPERANCE RIVER
SOUTH BRUNY
GREAT TAYLOR BAY
D'ENTRECASTEAUX CHANNEL
TASMAN HEAD
RECHERCHE BAY
0 1 2 3
SCALE IN MILES
147°15'
A.B.

Fig. 2.—D'Entrecasteaux Channel, showing area of investigations.

On the other hand, adjacent to Middleton the coarse sand grades through the fine sand until in the middle of Simpsons Bay the silt content of the sand is high. The reason for this distribution is readily understandable, for in the narrower region between Gordon and Middleton the strong tide (1-2 knots) sweeps away the finer sand, depositing it as its velocity decreases in the wider approaches. The higher silt content of the sand in the middle of the bay decreases shorewards.

IV. Results

(a) *Depth Range*

Three species of scallops are present on the commercial beds in the D'Entrecasteaux Channel. The "commercial" scallop, *Notovola meridionalis* (Tate), the upper valve of which is flat, is the most common and of greater commercial importance than either the "queen" scallop, *Equichlamys bifrons* (Lamarck), or "doughboy", *Mimachlamys asperrimus* (Lamarck). The first is bisexual and the other two are unisexual and have both valves curved.

On the extensive 7-fm mid-section of the Channel (the main scallop beds) the commercial scallop is found everywhere, whereas along the edges of the two end sections of the Channel they are aggregated into "strips". Because the concentration is greatest between 4 and 8 fm it is believed that within these depth limits environmental conditions are optimal for development and the scallops flourish. Throughout the Channel area it was repeatedly noticed that the maximum concentration was confined to the 4-8 fm contour. On the scallop beds of the open bays (Hazard Beach, Freycinet Peninsula (Fig. 1)) the range in depth is slightly more limited, being confined to 5-7½ fm; outside these limits the concentration fell rapidly.

In the D'Entrecasteaux Channel it was observed that the sea wrack *Zostera tasmanica* Mart. grows thickly from low-tide mark down to 2½-3 fm, where growth stops abruptly. Occasional tufts of leaves may occur out to 3½ fm but are not common. The presence of the sea wrack has proved a useful indicator of shallow depths.

Unlike the commercial scallop, which is mostly found on smooth bottom in waters 4-11 fm in depth, the queen scallop appears to occupy a much shallower range, from about 1 to 7 fm. Though this lower depth may be exceeded the queen scallop is more prevalent in shallower waters, for it may be found in association with the sea wrack in waters as shallow as 1 fm. It is a scallop which prefers undisturbed conditions, for it occurs not only in the above association but also in close proximity to reefs and rocky outcrops where dredging is hazardous and the bottom undisturbed.

Doughboy scallops have much the same depth range as commercial scallops, being found in common association with them. Not infrequently they are attached by a byssus to the flat valves of empty scallops.

(*b*) *Resting and Swimming Behaviour*

All three species rest on the sea floor. They do not bury themselves in the bottom, though they may occur in saucer-shaped depressions. These have been excavated gradually by the scallop's forcibly ejecting water from all around the gape. The silt builds up along the rim, forming a depression. If inactive scallops have been lying in these depressions for any length of time the upper valve may be covered by tide action with a thin deposit of fine sand and/or silt.

Probably it is this condition which has given rise to the incorrect belief that scallops bury themselves in the sea floor. The size of the depression is dependent on the degree of inactivity of the scallops, and type of bottom, for the higher the silt content the greater is its diameter and depth. Queen scallops form the largest depressions.

In the normal resting position the commercial scallop lies on the curved valve with the flat valve uppermost and on it are found epizoic growths. The gape of the valves is about $\frac{1}{2}$-$\frac{3}{4}$ in. wide, with the mantle edges inclined slightly inwards so that the many eyes are prominently displayed and the numerous short and long tentacles fully extended. Dakin (1909) has described fully the morphology of the mantle. Unless there is a very strong tide running the orientation of the shell gape is haphazard but in a strong tide the hinge faces into the tide. On two occasions scallops were found pulled over; either on their edges, hinge uppermost, so that the flat valve was at an acute angle to the sea floor, or lying on the flat valves. This was due to a red seaweed, *Griffithsia flabelliformis* (Harvey), attached by a single holdfast to the flat upper valve, streaming in the tideway.

The commercial scallops are the most active swimmers, the doughboy being only slightly less so, and the adult queen the most sedentary. Small queens seem to be vigorous swimmers.

The mode of swimming has been described previously (Dakin 1909). When commercials begin swimming, lips foremost, water is vigorously ejected behind in two narrow streams from either side of the hinge. The presence of these twin jet streams is apparent from the explosive disturbance created in the bottom sediments. At the beginning of their swim the scallops make an angled rise of about 6-18 in. in jerky fashion before they level off and swim parallel to the sea floor for horizontal distances up to 15 ft (measured). Some scallops have been observed to rise as high as 6 ft off the sea floor. The rate of closing of the two valves is fairly constant, for with each snap or "bite" the scallop moves forward about its own length. Some measurements carried out showed that it required about 12 bites to cover 3 ft. The small scallops (0+ and I+ age groups) appear to move proportionately faster than the adults. At the end of the swim a scallop closes the valves and falls gently by a side-slipping or zig-zag motion to a resting position on its curved surface, though it has been observed to fall on the flat upper valve. Rarely in nature do they move with the hinge foremost.

(*c*) *Reaction to Light and Movement*

In their own environment some observations were made of the reaction of scallops to light and movement. The effect of light on aquarium specimens has been critically reviewed by Gutsell (1930). They are apparently reactive to the diver's approach, for they either close up or swim away. Those scallops remaining quiescent either eject the water from all around the gape or gently in two broad streams from the hinge area. However, if approached from the hinge position and the measuring stick placed directly in front of the shell to shade only a few eyes, the scallops often showed no reaction; but if the stick was waved in front of the scallops so that most of the eyes perceived the movement, the molluscs either closed their valves or swam away. Rawitz (1888), quoted by Gutsell (1930), noted similar behaviour in aquarium specimens. Scallops will eject water from one side only in order to screw around prior to swimming. They will also swim in an upward curve by differential expulsion of water from the hinge area. The differential expulsion was gauged by the disturbance of the bottom caused by the two jet streams.

While walking beside or held suspended over dredges it was possible to watch the avoidance reaction of scallops. Those in the path of the dredge attempted to avoid it by either swimming upwards or sideways. Those which at the approach of the dredge closed their shells and remained inactive were caught, and the number scooped up during each dredge run is a measure of their reaction. It was observed from samples opened and examined under water that those scallops with muscle tissue in "good condition"* were the active swimmers and thereby escaped, whereas those with the adductor muscle lacking in condition closed up and were more easily caught. Scallopers beginning their dredging gauge the possibilities of new "strips" by the condition and number of scallops caught initially.

It was apparent from all underwater observations that the condition of the muscle determines the mobility of the scallop and this observation has been correlated with dredging tests.

It is customary for several scallopers to dredge in echelon formation on selected sites of good-quality scallops, for some contend that it is necessary to "dig out" the buried molluscs and get them "working". They believe that scallops bury themselves like their relatives, the clams, despite their obvious anatomical differences. However, what really happens is that they stir the scallops into activity. The scallops perceiving the movement of, or seeing the disturbance created by, the approaching dredges avoid them but eventually muscle fatigue prevents them from moving and they are caught in increasing numbers. It is common knowledge amongst the scallopers that they have to get good-quality scallops "working" for a couple of hours before they can catch them in quantity. Strictly speaking, they are fatiguing the scallops before dredging them up. The better the condition and quality of the scallop the longer the required period of "working".

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* Criteria for assessing condition in scallops are texture and colour of the large adductor muscle.

In certain areas such as Great Taylor's Bay, it is virtually impossible to make daylight catches, whereas by dredging during the hours of darkness good payable hauls are made. From these and other observations it is deduced that the scallops, being unable to sense the approaching dredges, are scooped up more easily at night. These areas usually have good sandy bottoms which reflect light and the scallops found there are of very good quality.

(*d*) *Distribution*

(i) *Juveniles.*—There are many conflicting theories about occurrences of large populations of juvenile scallops. It has even been postulated that there are "feeder beds" from which migration takes place to the recognized scallop fishing areas. The location of large numbers of juveniles is one of the difficult problems in scallop research. Fairbridge (1953, p. 36) drew attention to the absence of recruitment to the scallop stocks in the D'Entrecasteaux Channel during the period 1944 to 1949. However, in June 1950 a bed of these small scallops (modal length 28-30 mm) was found by scallopers. It was located in the area of an eddy current off Mountain Creek below Gordon (Fig. 2) and was not present in July 1947. It was subsequently found that there had been a concentrated spatfall in this position, and a limited but even fall over the greater portion of the main beds in 1948. In 1954 the presence of 5-15 mm juvenile scallops (0 + years) on the Mountain Creek bed may have indicated that a very limited spatfall took place there in 1953. These very small sizes were collected during diving observations by the writer.

The bed of juveniles off Mountain Creek was sampled with dredges at approximately 2-monthly intervals from June 1950 for the following 2 years and less frequently thereafter, and its population density was checked by diving observations each summer from 1951 to 1954. It was found that there was no movement of scallops away from this new bed, which did not alter its position. The dredged samples collected regularly from this bed showed that the scallops were generally slightly smaller than elsewhere. It is believed that the smaller size was due to overcrowding.

It may be presumed therefore that although scallops spawn regularly each year, successful spatfalls are very irregular. Yamamoto (1950) found only one in the decade 1941-1950, and our intensive efforts to locate beds of juveniles in the Channel from 1944 to 1954 confirm this irregularity of spatfall. We too have had only one such occurrence in a decade. Anecdotal evidence from scallopers of long experience indicated that these thickly populated beds of juveniles are of uncommon occurrence. Length frequency studies on scallops from various beds show that the fishery is dependent on heavy brood strengths, some of which sustain the annual 3-month fishery over a period of 7-9 years (Fairbridge 1953). Such data give added support to the theory that successful spatfalls are of sporadic occurrence, for reasons as yet unknown. It is suspected that they occur only when there is a delicate balance in a set of favourable environmental conditions.

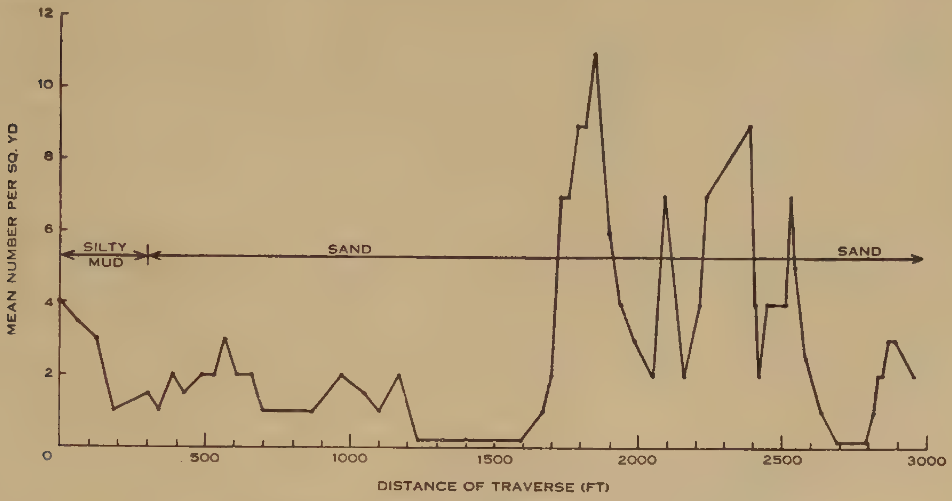

Fig. 3.—Distribution of scallops, Sheepwash Bay, June 19, 1951.

(ii) *Adults.*—The aggregation of scallops into "beds" or "strips" has led scallopers to believe that these shellfish occur in sharply defined, discrete communities between which there are barren tracts. Such is not the case. Diving observations have shown that scallops are distributed all over the large 7-fm area in the Channel, but *in varying concentrations.* These beds or strips are not discrete communities separated by barren tracts of the sea floor, but instead represent areas of high concentration of scallops. These areas may be a few to 100 or more feet in length and width. For no apparent reason there are sudden changes from areas of very low concentration to areas of high concentration. There do not appear to be any differences, which can be detected, in the structure of the bottom or the general ecology of the flora and fauna which would account for such sharp changes in population density. The scallops may be found on any type of bottom, such as silt-sand, fine sand, shell, or coarse sand and shell. Although small differences in depth appear to have no noticeable effect on an evenly distributed concentration of scallops, a sharp decrease was observed in the population density of a 1-2 fm gutter in an otherwise flat 7-fm area (Missionary Bay).

Figure 3 demonstrates the suddenness with which population densities in any area may change. The estimates of the number of scallops/sq. yd throughout the traverse were obtained by the method described in Section II.

This slightly zig-zag traverse of 3000 ft at a depth of 44 ± 2 ft was made in Sheepwash Bay on June 19, 1951. An area approximately 800 ft wide carried up to eleven scallops/sq. yd (mean, six scallops/sq. yd), whereas in the areas adjacent to it the mean concentration was less than one/sq. yd. The first 300 ft of the bottom was silty mud, which gave way to sand over the remaining distance. The scallops located between 0 and 1700 ft and between 1900 and 3000 ft of the traverse carried a heavier deposit of silt on their upper valves than those between 1700 and 1900 ft, whilst the scallops located between 2100 and 2240 ft exhibited an added characteristic of lying in deep depressions. There was no apparent explanation for this latter behaviour.

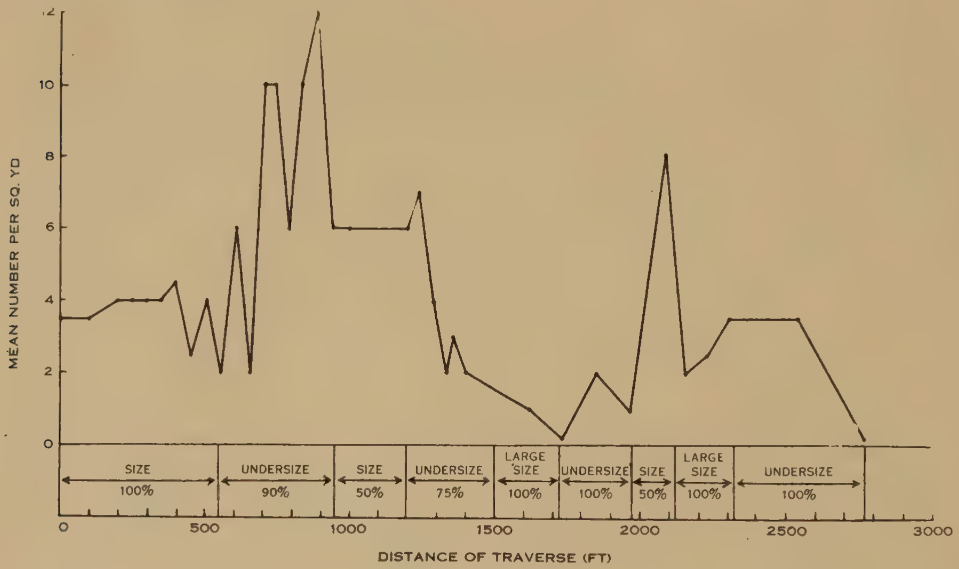

Fig. 4.—Distribution of scallops showing width of strips, Fisherman's Haul, June 20, 1951.

The area of high concentration was located in a strong tide flow, judging by the tide effect on the marine growth and our increase in speed over the bottom from 18 to 45 ft/min. Initially the speed was 30 ft/min and this dropped and rose again, the reason being the tide deflection caused by the points of the bay. The wind was relatively steady throughout and engine speed constant.

In this particular traverse no attempt was made to determine the vessel's course relative to the true width of the bed (high concentration of scallops). The experiment was designed to show the sudden and apparently inexplicable changes in concentration of scallops.

The following day another traverse was made nearby at Fisherman's Haul (Fig. 4). On this occasion the traverse was virtually at right angles to the shore and tide, the bottom was uniformly sand, and the depth was 39 ± 4 ft. Even though scallops of different year classes (1948, 1940, and earlier) were present throughout this traverse of 2800 ft, similar sudden changes in concentration occurred in the two predominant 1940 and 1948 broods. Only the 1948 year class ("undersize") was below the minimum legal size; the varying proportions of the year classes are indicated on Figure 4 by "size" (1940) and "large size" (year unknown).

Again, there was no noticeable difference in the configuration of the bottom carrying the varying concentrations of the same or different broods of scallops. It is believed that the estimated widths of the different scallop densities were correct, for the traverse was at right angles to the tide and shore and our course was made under power. Throughout all diving investigations it was observed that the strips or beds tended to lie with their long axes parallel to a flow of tide or along contours in the sheltered bays.

The same year class scallops from the two locations mentioned above have an almost identical mean length. Both these areas are in a strong tideway about a mile apart. However, near Fancy Bay (Fig. 2) scallops close inshore were significantly larger (mean 80 mm) than those of the same age group 500 ft out from the shore (mean 76 mm). The bottom was sandy throughout and the depth even at 34 ± 2 ft. The concentration of scallops of the same brood stock remained the same (six/sq. yd) throughout the 1400-ft traverse towards the centre of the bay. The even drift rate of 23 ft/min enabled the divers to cover this distance in an hour. Although the population density remained identical, the scallops appeared smaller in the latter half of the traverse and measurements confirmed this observation. All carried a thin deposit of silt and sand on the upper flat valve, they were less active, and greater numbers were in saucer-shaped depressions. A second traverse close to and parallel to the first confirmed this average difference in size. A veteran scalloper present at the time drew the writer's attention to the difference in condition of the main adductor muscle (scallop meat) between those close inshore and those further out. The inshore scallops had a firmer, whiter muscle which was more compact than the flabby, watery tissue from the scallops nearer the centre of the bay. The gonads too were further advanced in the former.

In a square mile of the area near Fancy Bay there was an estimated population of 18 million scallops. This number is derived from the observed concentration of six scallops/sq. yd and the size of the known bed, which is the most extensive yet encountered in the course of these investigations.

It appears from the underwater studies that tides have a most important effect on the distribution of larvae and their final settlement. In areas of strong tides we find strips or beds of varying widths of the same brood of scallops running lengthwise to the tide, but where the tides are weaker we encounter a much more evenly dispersed population over a greater area (Fancy Bay). Then again in eddy systems we find the high-concentration beds (30-36 scallops/sq. yd) like that of the juvenile bed off Mountain Creek near Gordon.

The tide has a marked influence not only on the setting of the planktonic scallop larvae but also on their subsequent growth and condition. In the area between Middleton and Gordon, where the tides are always stronger than elsewhere, better-quality scallop meats are obtained and the shell structure is harder and more compact. In the Fancy Bay area there is the difference in condition between the scallops close inshore and those nearer the centre of the bay; and as the latter scallops age they develop brittle shells which break easily, and these are not liked in the trade. The brittle condition of the shell is not so evident amongst the scallops closer inshore. Gutsell (1930) noted that areas of strong currents in Bogue Sound, North Carolina, produced larger and faster-growing scallops.

Further evidence, though circumstantial, in support of this theory of the importance of tide (water movement) is obtained from other areas, for it has long been recognized by scallopers that catches made in areas of strong tides yield not only the bigger and faster-growing scallops but also those in prime condition.

Scallops from open bays such as Norfolk Bay, or Oyster Bay near Hazard Island off Freycinet Peninsula (Fig. 1), tend to have thicker and heavier shells than those from the Channel; moreover the average meat yield per 1000 scallops in 1954 was greater from the open bays (36 lb) than from the Channel (30 lb).

The Hazard Island scallops were found to occur in a more limited depth range, the highest concentrations being found between 5 and 7 fm, but otherwise their general ecology is identical with that of the scallops from the D'Entrecasteaux Channel.

On a number of occasions in suitable locations large holes have been dug in the sea floor among high concentrations of the same brood year scallops. The sizes of the partially buried dead scallops were similar to those of the living ones but as the overlying debris was removed it was seen that the lengths of buried shells became progressively smaller down to about 30 mm. These small shells immediately overlay large shells, the lengths of which ranged from 90 to 100 mm. These large shells occurred 6-8 in. below the present level of the sea floor and provide additional evidence supporting the theory of random sporadic spatfall. Had this settling been regular no such decreasing gradation in size would have been evident.

(*e*) *Minimum Economic Concentrations*

During the middle of the 1951 scallop season (June) a descent was made on the centre of a strip worked by 14 boats. This strip had sustained the fishing vessels for almost 5 weeks previously and the catch from it was fast declining. Within a week the fishing effort was transferred elsewhere. It was found that the concentration was down to two scallops/sq. yd. The scallopers expressed the opinion that the catch from this area represented the lowest concentration on which they could work. Had it not been for the good meat yield (roe included) of 33 lb/1000 scallops, fishing would have ceased.

In view of this information and the knowledge that the area had been intensively fished, the value of two scallops/sq. yd has been accepted as the minimum economic limit.

(*f*) *Predation*

Throughout this study only two predators of scallops were observed. The greatest damage to the scallop stocks is caused by the large eleven-armed spiny starfish *Coscinasterias calamaria* (Gray), which grows up to 18 in. across. In this species, which has a small disc (2 in.), the long thick arms, each bearing numerous tube feet, envelop the scallop and pull apart the valves, enabling the protrusible thin-walled stomach to enter the gape in the valves.

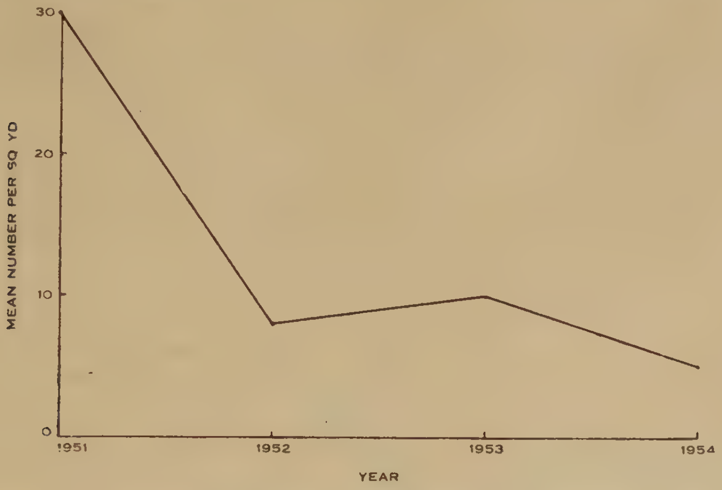

Fig. 5.—Decrease in scallop concentration off Mountain Creek resulting from starfish predation.

All stages in the digestion of the soft parts of the scallop have been observed. Starfish are well known as predators of shellfish.

The other predator, the large whelk or band shell (*Fasciolaria australasia* Perry), though widely scattered on the scallop beds, was found only once in the process of digesting an adult scallop.

The destruction to the stock of scallops on the Mountain Creek bed considered to be wrought by starfish in 4 years has been assessed at 75-80 per cent. This mortality value was derived from the March 1951 concentration of 30-36 scallops/sq. yd and that of April 1954, when the number had been reduced to five scallops/sq. yd. Figure 5 shows the progressive reduction in the number of scallops, due primarily to starfish predation.

The greatest number of starfish on any bed was found on the Mountain Creek bed in 1951, when there was one starfish to 25 sq. yd. Since then the number has gradually declined. It has been found that areas of high concentration also carry the most starfish. This is readily understandable, for the starfish would naturally tend to concentrate in the areas of greatest availability of food. Their preference seems to be for juvenile beds, for whereas they digest only the soft parts of half to fully grown adult scallops, all the flesh of the smaller scallops is digested. The starfish leave only the empty shell of juveniles whereas the adductor muscle is mostly left in the larger scallops.

It has been claimed by fishermen that the bay flathead (*Trudis bassensis* Cuv. & Val.) is a predator because this teleost is caught with scallop meats in the stomach. However, there are no gills and soft parts attached to the white muscle of the scallops taken from the flathead stomachs, and dead scallops with only the adductor muscle in the shell have been dredged. From these observations it is deduced that the flathead only remove the muscle from the gaping valves of the partly digested scallop *after a starfish has first digested the soft parts.* The flathead is able to push its long flat snout into the gape of the valve and swallow the white adductor muscle.

When the writer has been opening and examining scallops under water there have been at times up to 50 flathead following and snapping up the discarded scallops. Opened scallops, still attached to one valve held in the hand are taken by flathead. This experiment has been repeated on numerous occasions and witnessed by other divers.

At no time has the writer seen flathead even attempting to eat live scallops.

V. Discussion

Unlike so many fishery investigations where only the orthodox indirect methods are applicable, the scallop fishery, by virtue of its relatively static population, is admirably suited to direct assessment by diving. The scallops are spread out over the sea floor ready for counting, and it is possible to determine not only their numbers and population densities but also the proportions and limits of the different year classes. By selective sampling, ranges in sizes of the scallops in these classes can be determined as quickly and satisfactorily as by examination of the large samples (Table 1) brought aboard by dredging.

The term "cluckers" has been used for dead scallops, both valves of which are still joined (Dickie 1953).

Since Tasmanian scallops cannot be taken legally under a certain size (76 mm) and it has been observed that the scallops on the Mountain Creek bed required 6 years to reach that size, it is possible to forecast reasonably accurately the effect of a particular brood strength and the year it will become fishable. Until 1954 the fishery was dependent on stocks spawned in 1940 and 1941 (Fairbridge 1953). The catches of Digby scallops, *Plactopecten magellanicus* (Gmelin), are likewise influenced by the strengths of the various year classes, the 1952 fishery being dependent on brood strengths produced in 1939, 1940, 1945, and 1946 (Dickie 1953).

Yamamoto (1950) found that a very large concentration of small scallops had developed from a successful spatfall in Mutsu Bay in 1948, and this strong year class was the first substantial recruitment observed during his 10 years of study. Other workers—Priol (1929) working on French scallops, Tang (1941) and J. Mason (personal communication, 1953) on Isle of Man scallops, and Baird (1952) on English Channel scallops—reported the virtual absence of young scallops during the course of their investigations. With such evidence accumulating from widely scattered sources, it must be concluded that although scallops spawn every year, successful settling, establishment, and eventual development of spat is not only very sporadic but unpredictable in our present state of knowledge.

TABLE 1

COMPARISON OF SIZES IN TWO YEAR CLASSES ON THE SAME BED (SHEPPARDS)

Age and Condition	Diving (28.iv.1952) Size Range (mm)	Sample No.	Dredging (13.iv.1952) Size Range (mm)	Sample No.
Dead juveniles, 1948 stock ("cluckers")	32-43	5	34-50	7
Living juveniles	55-71	41	61-77	300
Living adults (1940-1941 stock)	80-105	18	79-104	50

There have been no apparent unusual hydrological conditions to account for the good spatfall of scallops in certain areas in the D'Entrecasteaux Channel in 1948. The high density off Mountain Creek in 1951 (36 scallops/sq. yd) compared favourably with the actual spatfall count of 50-250/sq. m for *Pecten yessoensis* (Jay) in Mutsu Bay (Yamamoto 1952). It is believed that an eddy had the effect of concentrating this spat, and Orton's (1937) observation on *Cardium edule* L., when 100,000 spat/sq. m were deposited by an eddy current, supports this theory of concentration. In other areas where the current is strong the scallops are located in long strips parallel to it or evenly distributed where the water movement is slow (Fancy Bay).

At the start of this investigation scallop fishermen reported that juveniles, or "buttons" as they call them, were plentiful off Mountain Creek "a few years ago", and it is now believed that the density was a result of the strong 1940 year class being concentrated there. However, despite diligent searching none could be found in 1947, and had they been present their concentrations would have made them obvious since it is possible to detect the presence of 0+ scallops (5-15 mm) even in small numbers. At first it may seem improbable that such small scallops could be seen, let alone picked up. However, it must be remembered that underwater objects are magnified and the diver's attention is drawn to these small scallops by the slight disturbance of the flocculent silt caused by their expelling water from between their valves. Not until 1954 were these very small sizes found.

Although adult scallops have mobility there is no evidence to suggest that they migrate, causing a bed or strip to move or disappear. From these observations it seems that the width of the area of high concentration of scallops is a function of the tide or current strength at the time of settling of the metamorphosed scallop larvae. Once a scallop bed or area of high population density becomes established, it remains static throughout the life of the individuals unless affected by such external influences as violent storms or fishing by man. The former presence of scallop beds does not necessarily mean that scallops may always be found in the same or nearby positions. Scallops die from senility (inferred from presence of extensive beds of very old scallops apparently dying from natural causes), and throughout the life of the scallops conditions may not be suitable for a spatfall large enough to replenish the stocks. There is ample evidence to indicate that some such effect must have been responsible for the disappearance of known beds in certain bays and estuaries around the Tasmanian coast, for where formerly scallops were dredged in quantity only dead shells can now be found (Ralphs Bay, Derwent River, and off Babel Island).

Concern has often been expressed about the stocks of scallops in the D'Entrecasteaux Channel and conservation measures such as closing certain areas have been advocated. However, it is well recognized that fishing never exterminates a stock but reduces the stock to individuals of minimum legal size and/or an uneconomic level of operation. Therefore so long as there is an ample breeding stock of those below the minimum legal size, any proposal restricting areas of dredging is preventing the rational exploitation of a fishable stock. If recruitment is negligible, i.e. no successful spatfall, and the previously undersized breeding stock becomes fishable the numbers of scallops below the minimum economic limit should be sufficient to constitute a breeding stock. If the circumstances are such that there is no successful spatfall the scallop bed then ceases to exist, but there seems little danger of this occurring in the Channel. Had there been an enforced closure such a bed of scallops would have died in any case and the shellfish would have been unavailable as food. Closing of beds as a conservation measure for scallops is considered undesirable so long as the minimum size is strictly enforced.

The conclusion that the life expectancy of any year class in the D'Entrecasteaux Channel is limited to a maximum of 15-16 years is based on observations made over widely separated areas which showed that after 14 years the 1940 year class is poorly represented on the beds and that the present fishery is supported by the 1948 year class.

VI. ACKNOWLEDGMENTS

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Mr. D. E. Kurth, Mr. J. C. Dowsett, and Mr. W. A. Turner were variously responsible for recording the data.

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TRACHYMEDUSAE AND NARCOMEDUSAE OF SOUTH-EAST AUSTRALIAN WATERS

By M. BLACKBURN*

(*Manuscript received January 26, 1955*)

Summary

Thirteen species of Trachymedusae and seven of Narcomedusae are recorded from south-east Australian waters, where both orders were previously unknown. Eight Trachymedusae and four Narcomedusae are new records for the entire Australian region. Additions are made to the descriptions of some species.

Eight species are epipelagic, seven bathypelagic, and five probably eurybathic in the upper 1000 m of the sea; the second and third groups contain several cosmopolitan species, but the species of the first (epipelagic) group tend to be restricted to tropical and subtropical latitudes. One epipelagic species, *Liriope tetraphylla* (Chamisso & Eysenhardt), has not been found south of lat. 39° S. in south-east Australian waters and may serve as an indicator of one of the two main water masses which meet in that region.

The most abundant species of either order is *Aglaura hemistoma* Péron & Lesueur, which is the commonest of all hydromedusae on the continental shelf off Queensland and New South Wales. *Aglaura* and *Liriope* are also recorded from the neighbourhood of Fremantle, W.A.

I. INTRODUCTION

Kramp (1953) drew attention to the scanty knowledge of Australian hydromedusae, and an attempt is now being made to classify those which occur in the plankton of the south-east Australian region. It is natural to consider first the orders Trachymedusae and Narcomedusae, which are holoplanktonic and mainly oceanic, and thus might be expected to serve as indicators of sea-water masses.

According to the useful review of previous work on Australian hydromedusae by Kramp (1953), the authors who preceded him (Péron and Lesueur 1809; Quoy and Gaimard 1824; Haeckel 1879; Mayer 1915) may be credited with recording five species of Trachymedusae and two of Narcomedusae from various Australian waters. In the same publication Kramp himself recorded four of these Trachymedusae and one of the Narcomedusae again, from the neighbourhood of Low Isles on the Great Barrier Reef; and added two more species of each order, all from Low Isles, to the Australian list. This list then stood as follows:

Order **TRACHYMEDUSAE**

Family **GERYONIDAE**

**Geryonia proboscidalis* (Forskål): NW. Australia, Low Is.
**Liriope tetraphylla* (Chamisso & Eysenhardt): Torres Str., Low Is.

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Family RHOPALONEMATIDAE

**Rhopalonema velatum* Gegenbaur: Torres Str., Low Is.
**Aglaura hemistoma* Péron & Lesueur: Arnhem Land, Torres Str., Low Is.
Stauraglaura tetragonima Haeckel: "Australia".
Amphogona apsteini (Vanhöffen): Low Is.

Family HALICREIDAE

**Halicreas minimum* Fewkes: Low Is.

Order NARCOMEDUSAE

Family SOLMARIDAE

**Solmaris rhodoloma* (Brandt): Low Is.

Family AEGINIDAE

Aeginura myosura Haeckel: Lat. 47° 25′ S., long. 130° 32′ E.
**Solmundella bitentaculata* (Quoy & Gaimard): Torres Str., Low Is.

Family CUNINIDAE

**Cunina octonaria* McCrady: Low Is.

It will be seen that no species has previously been recorded from the south-east Australian region. In the present paper 13 species of Trachymedusae (including five marked* in the list above) and seven of Narcomedusae (including three marked* in the list above) are recorded from those waters. The 12 additions to the Australian fauna are as follows:

Order TRACHYMEDUSAE

Family RHOPALONEMATIDAE

Sminthea eurygaster Gegenbaur.
Colobonema sericeum Vanhöffen.
Pantochogon haeckeli Maas.
Aglantha elongata (Lesson).
Persa incolorata McCrady.

Family HALICREIDAE

Haliscera conica Vanhöffen.
Halitrephes valdiviae Vanhöffen.
Botrynema brucei Browne.

Order NARCOMEDUSAE

Family AEGINIDAE

Aegina citrea Eschscholtz.

Family CUNINIDAE

Cunina rubiginosa (Kölliker).
Cunina duplicata Maas.
Solmissus marshalli Agassiz & Mayer.

The following groups of plankton collections were examined for medusae. In all but the second group the sorting was done by the writer. Either the whole or a nine-tenths subsample of each catch was sorted, the difference being unimportant for the purpose of this paper.

(1) Open horizontal hauls made with the "Discovery" N200 net at various depths from 100 m to the surface, from F.R.V. *Warreen* at several stations on the continental shelf and on the continental slope immediately

beyond the shelf, in the northern waters of New South Wales and the southern waters of Queensland, in September 1938.

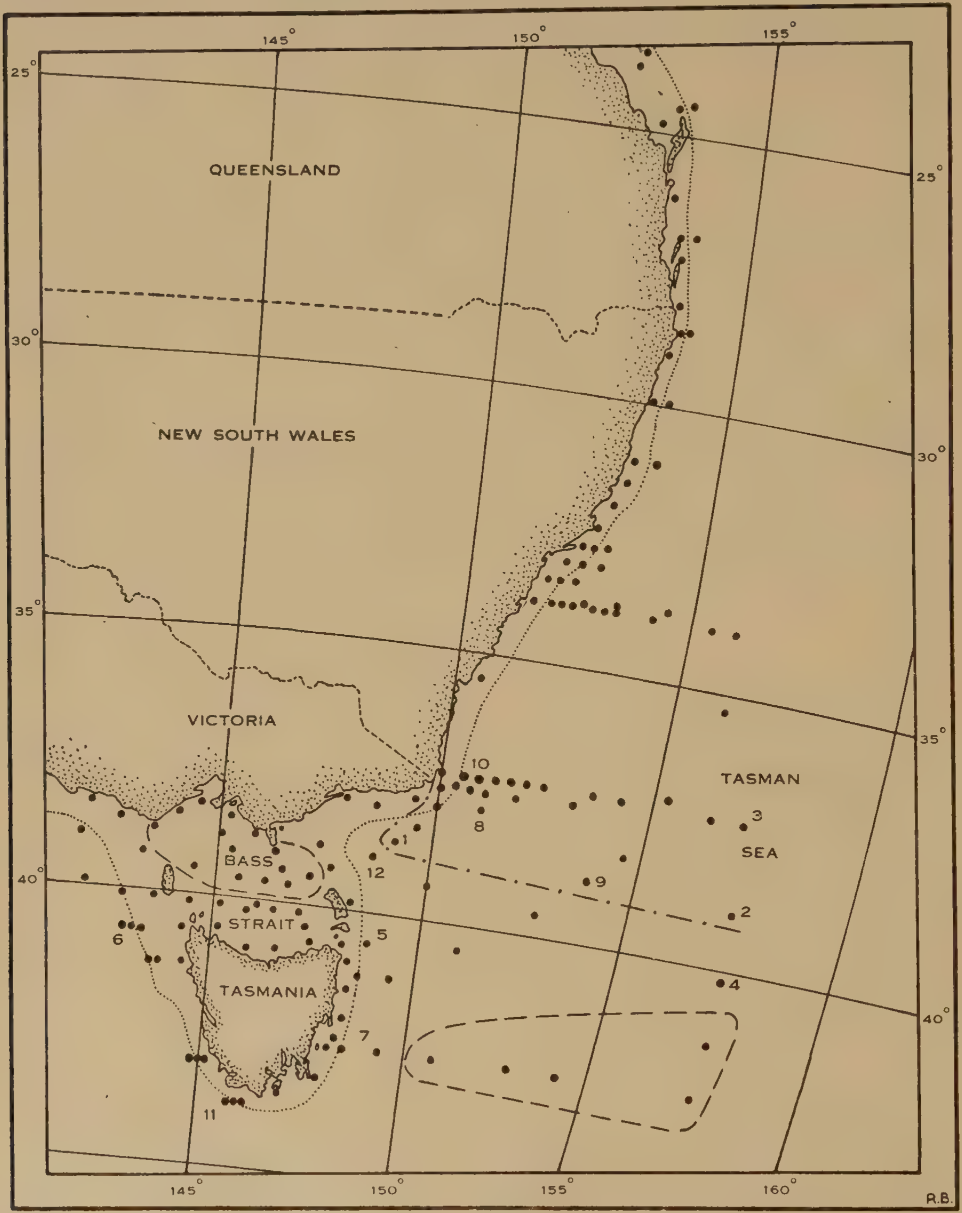
145°
150°
155°
25°
30°
35°
40°
160°
QUEENSLAND
NEW SOUTH WALES
VICTORIA
BASS
STRAIT
TASMANIA
TASMAN
SEA
1
2
3
4
5
6
7
8
9
10
11
12
R.B.

Fig. 1.—Stations occupied in plankton investigations; see text for references to numbered stations (1-12). ..... Edge of continental shelf; —— enclosing areas yielding no specimens; —.—. southern boundary of *Liriope tetraphylla*.

(2) Open oblique hauls made with the "Discovery" N100 net from depths not exceeding 154 m to the surface from R.R.S. *Discovery II* at her

stations 2706 to 2725 (New South Wales coast and 200 miles seawards in lat. 34° S. and 37° S.) in October 1950.

(3) Vertical hauls (mostly open) made in duplicate with the "Discovery" N70 net on the continental shelf from bottom (generally 50-60 m, not exceeding 100 m) to surface, from F.R.V. *Derwent Hunter* and other vessels at several stations in most parts of the waters of New South Wales, Victoria, and Tasmania, from January 1952 to December 1954. The stations were occupied about four times a year on an average, at irregular intervals, those in New South Wales waters being the best attended.

(4) Open and closed vertical hauls made with the N70 net from F.R.V. *Derwent Hunter* at a few stations on the edge of the continental shelf and on the continental slope up to 20 miles beyond the edge, in the waters of central and southern New South Wales, Victoria, and Tasmania, from August 1952 to December 1954. The open hauls were made from varying depths (200-500 m) to the surface, in duplicate, and from 50 m to the surface. The closed hauls were made regularly at the slope stations from 500 to 400, 400 to 300, 300 to 200, 200 to 100, and 100 to 50 m; when time permitted an additional haul was started at some much greater depth (maximum 2200 m) and closed at 500 m. Only a few visits, from one to six for each station during the two years, were paid to these stations.

(5) Closed and open vertical hauls (500-300, 300-100, 100-50, 50-0 m) and surface horizontal hauls made with the N70 net from the F.R.V. *Derwent Hunter* in February 1954, at 30 stations in various parts of the south-west Tasman Sea between lat. 34° S. and 43° S. and long. 148° E. and 157° E. up to 350 miles from the eastern Australian coast; and open vertical hauls (500-0, 100-0 m) made with the N70 net from the same ship at 24 stations in the same region in November and December 1954.

The positions of all these stations are shown in Figure 1. Two large clusters of stations which yielded no specimens are distinguished there. It is unnecessary to give further details about the sources of the medusa material, except for notes under each species below. Enough work was done to be expected to reveal most of the species present, their gross abundance and distribution by area, and something of their bathymetric distribution, although not their seasonal distribution.

II. List of Species

Order TRACHYMEDUSAE

Family GERYONIDAE

GERYONIA PROBOSCIDALIS (Forskål)

Medusa proboscidalis Forskål, 1775, p. 108.

Geryonia proboscidalis Mayer, 1910, p. 425, fig. 282; pl. 53, figs. 1-3; pl. 54, fig. 10. Thiel, 1936, p. 53. Kramp, 1953, pp. 301, 308-9.

Only one specimen, 5 mm in diameter, was taken. It was obtained in a horizontal haul at 100 m (and thence, with the net open, to the surface) at the slope station off Sandy Cape, Qld. (Fig. 1, lat. 24° 35′ S.).

This species has been recorded from Endracht's Land in north-western Australia (Quoy and Gaimard 1824, as *Dianaea endrachtensis,* see Kramp 1953), the "coast of Australia" (Haeckel 1879, as *Carmaris giltschi,* see Kramp 1953), and Low Isles (Kramp 1953), but not from any Australian water south of lat. 25° S. *G. proboscidalis* is widely distributed in all three oceans between lat. 35° N. and 35° S., and occurs in the Mediterranean. It is generally found near the surface, although Thiel recorded a fragment, which was possibly dead and sinking, between 400 and 600 m.

LIRIOPE TETRAPHYLLA (Chamisso & Eysenhardt)

Geryonia tetraphylla Chamisso & Eysenhardt, 1821, p. 357.

Liriope tetraphylla Thiel, 1936, p. 45. Kramp, 1953, p. 301. Russell, 1953, p. 419, figs. 275-282; pl. 24, fig. 2.

The author accepts the view of Thiel, Kramp, Russell, and others that there is only one good species of *Liriope.* It was encountered at almost all south-east Australian shelf stations, and several slope and ocean stations up to 300 miles offshore (e.g. stations 1 and 2 in Fig. 1), as far south as lat. 38° 45′ S. It was there the second most common medusa of these two orders (next after *Aglaura hemistoma*; see below), although no more than seven specimens were taken in any of the bottom-to-surface vertical hauls which were made in depths from 50 to 60 m. Young specimens (1-5 mm in diameter) were much commoner than old. As all specimens from the slope and ocean stations were taken in open hauls, there is nothing to add to previous observations on bathymetric distribution. The species is commonest in the uppermost 100 m of the sea, but Thiel has recorded it between 400 and 600 m.

The writer has also seen specimens of this medusa from the continental shelf off Fremantle, W.A. (lat. 32° S.). Mayer (1915) recorded it (as *L. rosacea*) from Torres Strait, and Kramp noted it from Low Isles. *L. tetraphylla* is widely distributed in all three oceans from about lat. 50° N. (English Channel) to 38° S., and in the Mediterranean.

Family **RHOPALONEMATIDAE**

RHOPALONEMA VELATUM Gegenbaur

Rhopalonema velatum Gegenbaur, 1856, p. 251. Mayer, 1910, p. 378, figs. 213-219; 1915, p. 202. Thiel, 1936, p. 10. Kramp, 1953, p. 299. Russell, 1953, p. 430.

As far south as lat. 39° S. the distribution of this species resembles that of *Liriope,* including waters as far offshore as station 2 in Figure 1; but it also occurs at shelf and slope stations in the eastern and western approaches to Bass Strait and on the east and west coasts of Tasmania, reaching lat. 43° 40′ S. (Fig. 1). It has not been found in the centre of Bass Strait, i.e. between the eastern and western island chains.

Specimens 1-8 mm in diameter, all clearly recognizable as this species, were taken. At 1 mm the first series of eight tentacles is complete and signs of the second series (small bulbs on the umbrella margin, between the radial canals) may be seen; at 1.5 mm both series are clearly recognizable, and medusae at both these sizes may have the conical thickening at the apex of the bell, and most other features (except gonads) of the adult *R. velatum.*

Most of the specimens were taken in open hauls, but on two occasions captures were made with the closing net between 200 and 300 m. Thiel found a specimen between 400 and 600 m, but it has generally been taken in the uppermost 100 m. The largest number of *R. velatum* taken in a bottom-to-surface vertical haul in 50-60 m was four; north of lat. 39° S. it is often taken with *Liriope,* but generally in smaller numbers, and the numbers in comparable hauls diminish further towards the south.

Mayer (1915) recorded this species from Torres Strait, and Kramp noted it from Low Isles. Thus it ranges from the most northerly to the most southerly Australian waters. It occurs in all three oceans from about 58° N. (west of Scotland) to 49° S., and in the Mediterranean.

SMINTHEA EURYGASTER Gegenbaur

Sminthea eurygaster Gegenbaur, 1856, p. 245. Mayer, 1910, p. 383, figs. 226, 227. Thiel, 1936, p. 17.

Twenty-eight specimens were obtained, 25 from slope and ocean stations and three from shelf stations. The ocean stations at which it was found are those numbered 3 and 4 in Figure 1, and the slope and shelf stations are scattered along the entire New South Wales coast, in the eastern and western approaches to Bass Strait (but not in the centre), and on the west coast of Tasmania. In its geographical range this species resembles the much commoner *Rhopalonema velatum,* but its bathymetric distribution is different; six specimens were taken in the well-sampled layer between the surface and 100 m, and one in each of the following strata: 100-200, 200-300, 400-500, and 500-650 m. The other 18 specimens were taken in open hauls from 500 m to the surface. Thiel recorded this medusa as far down as 800-1000 m and discovered it more often below than above 200 m depth.

Sminthea eurygaster differs from *Rhopalonema velatum,* with which it may at first sight be confused, in having only eight tentacles (one opposite each radial canal), which are all short and generally like those of *Colobonema sericeum* (see below), and globular or ovoid gonads, varying considerably in size, on the distal ends of the radial canals. The apical thickening of the bell, which is regularly found in *Rhopalonema velatum,* is occasionally seen in *Sminthea.* The manubrium is generally much shorter than that of *R. velatum,* averaging less than one-quarter of the height of the bell. The Australian specimens range from 2 to 6 mm in diameter, the smallest with recognizable gonads measuring 3 mm.

This species has not previously been reported from the Pacific or from any part of the Australian region. It has been found in the Atlantic Ocean from about lat. 50° N. (Bay of Biscay) to the sub-Antarctic (lat. 57° S., south of Tierra del Fuego), and in the Indian Ocean and the Mediterranean. The world distribution as now known resembles that of *Rhopalonema velatum*. Another species, *S. arctica* Hartlaub, has been taken in the Arctic Ocean; Thiel drew no distinction between this and *S. eurygaster*, but there is a marked difference in the gonads, which in *S. arctica* lie along the inner three-quarters of the radial canals.

COLOBONEMA SERICEUM Vanhöffen

Colobonema sericeum Vanhöffen, 1902, p. 57, pl. 9, fig. 1; pl. 12, figs. 39-42. Russell, 1953, p. 436.

Colobonema typicum Bigelow, 1938, p. 117.

Two specimens were obtained at slope stations east of Bass Strait (stations 1 and 5 in Fig. 1) in open vertical hauls from 500 m to the surface. One, 7 mm in diameter, is smaller and less developed than any specimen hitherto described; it has eight perradial tentacles and four adradial tentacles (one well developed, the others rudimentary) at equal intervals around the bell-margin. That is to say, four perradial tentacles with no adjacent adradial tentacles alternate with four perradial tentacles each of which is followed, at a distance of one-quarter of an octant of the bell-margin, by one adradial tentacle. This specimen has no gonads. The second specimen, 18 mm in diameter, has the full number of 32 tentacles, eight perradial, eight interradial, and 16 adradial, of which the eight interradial tentacles are very small and were obviously the last to appear; this confirms the observations of other authors on medusae of this species at a similar size. All tentacles are short, as described by other authors, and appear to be unbroken.

This species is known from the warm and temperate waters of the Atlantic, Pacific, and Indian Oceans, from about lat. 65° N. (Iceland) to 42° S., but not from the Mediterranean. It has not previously been found in the Australian region. It has been taken by nets hauled as close to the surface as 241-0 m, and as deep as 1500-900 m. Its centre of bathymetric distribution is probably below that of *Sminthea eurygaster*.

PANTOCHOGON HAECKELI Maas

Pantochogon haeckeli Maas, 1893, p. 17, pl. 1, fig. 2. Bigelow, 1938, p. 115. Russell, 1953, p. 440.

Five specimens were obtained at slope stations east of Bass Strait (stations 1 and 5, Fig. 1): four in one haul from 1650 to 500 m, one in a haul from 750 m to the surface. There is nothing to be added to previous descriptions. The tentacles of all specimens are short, as described by previous authors, but not of even length, and some appear to be broken; their natural size therefore remains in doubt.

P. haeckeli is truly world-wide, having been found in the Arctic and Antarctic Oceans as well as in tropical and temperate parts of the Atlantic, Pacific, and Indian Oceans and in the Mediterranean. It has not previously been recorded from the Australian region. It is a bathypelagic species, like *Colobonema sericeum*, although one specimen has been taken in the uppermost 60 m of the sea.

AGLAURA HEMISTOMA Péron & Lesueur

Aglaura hemistoma Péron & Lesueur, 1809, p. 351. Mayer, 1910, p. 398, figs. 250-253; pl. 46, figs. 4, 5, pl. 49, figs. 3-7, pl. 50, fig. 11; 1915, p. 160. Thiel, 1936, p. 39. Kramp, 1953, pp. 300, 307, 311.

This is by far the commonest representative of the two orders in south-east Australian waters. On the New South Wales coast, as at Low Isles (Kramp), it is the most abundant of all hydromedusae, being represented in the great majority of hauls at all times of year, sometimes in large numbers; the greatest number taken in a bottom-to-surface vertical haul with the N70 net in 50-60 m of water was 280 (cf. maxima of seven and four respectively for *Liriope* and *Rhopalonema* in similar hauls), and catches of over 20 per haul were fairly common. It also occurs in much smaller numbers far out in the Tasman Sea, as far south as lat. 40° S. (e.g. stations 2, 3, 4 in Fig. 1), and in most shelf and slope waters adjacent to the Victorian and Tasmanian coasts, down to lat. 43° S. It has even been found in the centre of Bass Strait (southern part), being the only species of Trachymedusae represented there, although so far found only in the autumn; but it has not yet been found off the west coast of Tasmania. Apart from these two regions, the general distribution of *Aglaura* in south-east Australian waters resembles that of *Rhopalonema velatum*.

The gonads of *Aglaura* first appear, as eight small globules on the peduncle, when the animal is about 1.5 mm high. Some doubt therefore must attach to the identification of several smaller specimens (down to 0.8 mm high) which have no gonads and might belong to the genera *Stauraglaura*, *Aglantha*, or *Persa*, which closely resemble *Aglaura* apart from the gonads. All these doubtful specimens were counted as *Aglaura*, since in almost every case they were taken together with indubitable *Aglaura*.

The deepest haul which yielded an indubitable *Aglaura* was from 200 to 100 m, in the western approaches to Bass Strait. Another specimen, which, however, had no gonads and might have been *Aglantha* or *Persa*, was taken from 500 to 400 m in the same region. All others were in the uppermost 100 m of water, or could not with certainty be assigned to any greater depth. Thiel recorded one specimen from 400 to 200 m, but found it most common near the surface.

Apart from the fact that the species was found in the centre of Bass Strait only in the autumn, no marked consistent seasonal change in abundance was observed. Kramp at Low Isles found moderate numbers in winter and spring succeeded by low numbers in summer and high numbers in autumn; there are indications that *Aglaura* is least abundant in the summer months in south-east Australian waters also, but the sampling has not been sufficiently regular at any station to place the matter beyond doubt.

Aglaura hemistoma has previously been recorded in Australian waters from Arnhem Land (Péron and Lesueur 1809, as *Pegasia cylindrella*; see Kramp 1953), Torres Strait (Mayer 1915), and Low Isles (Kramp 1953). As the present writer has seen specimens from the continental shelf near Fremantle, W.A., as well as throughout south-eastern waters, the species probably occurs in all Australian seas. It occurs in the warmer parts of the Atlantic, Pacific, and Indian Oceans and in the Mediterranean, the most southerly records being those from Tasmania mentioned above and the most northerly being from lat. 45° N. in the Atlantic.

AGLANTHA ELONGATA (Lesson)

Circe elongata Lesson, 1843, p. 286.
Aglantha elongata Mayer, 1910, p. 404, fig. 255.

Two specimens, taken on different occasions between 400 and 500 m at the same station east of Bass Strait (station 5, Fig. 1), appear to belong to this species. Each has eight gonads, which protrude into the cavity of the bell from about the centres of the descending portions of the eight radial canals.

The smaller specimen, 2 mm high and 2 mm in greatest diameter, has four tentacles in each octant of the bell-margin, and very small spherical gonads; the peduncle has been torn. The larger specimen, 4 mm high and 2.5 mm in diameter, has six tentacles in each octant; the peduncle is short, about 0.5 mm long, and the stomach and lips together measure about 0.5 mm; the gonads are irregularly sausage-shaped, about 0.5 mm long, each attached to the subumbrella at one end with the other hanging free in the bell cavity. Both specimens have a conical apex, and the tentacles of each medusa are all of the same size.

These specimens differ from *A. elongata* only in the shape of bell and length of peduncle, characters which are so variable in related species and genera that it would be injudicious to use differences in them for the recognition of a new species. The specimens are accepted as a valid new record of *A. elongata* for the Australian region. It has previously been recorded only from the west coast of Africa as deep as 800-1000 m (Maas 1904, p. 30, as *Agliscra elata*, in part; see also Kramp 1947, p. 27).

As mentioned above, it is possible that immature specimens of this species have been identified as *Aglaura hemistoma*, but it is very unlikely in view of the fact that *Aglantha* is bathypelagic and *Aglaura* epipelagic.

PERSA INCOLORATA McCrady

Persa incolorata McCrady, 1857, p. 104. Mayer, 1910, p. 408, figs. 259-262. Thiel, 1936, p. 43.

Five specimens were obtained from four slope and ocean stations in the south-east Australian region (stations 6-9 in Fig. 1). They range in height from 2 to 3 mm, with 32-40 tentacles on the bell-margin, and each has two gonads 180° apart, a short peduncle, and stomach up to half as long as the height of the bell. It is possible that some immature specimens of this species were wrongly identified as *Aglaura hemistoma*, although *Persa* tends to inhabit deeper waters than *Aglaura*. Two of the Australian specimens were taken between 500 and 1000 m, one between 300 and 400 m, and two between 500 m and the surface. Thiel recorded it as deep as 700-500 m and as shallow as 50-0 m, but mostly deeper than 200 m.

This species has not previously been taken outside the Atlantic, where it occurs between about lat. 40° N. and 40° S., and the Mediterranean.

Family **HALICREIDAE**

HALICREAS MINIMUM Fewkes

Halicreas minimum Fewkes, 1882, p. 306. Bigelow, 1938, p. 122. Kramp, 1953, p. 299. Russell, 1953, p. 452, figs. 299, 300.

Halicreas papillosum Vanhöffen, 1902, p. 68. Mayer, 1910, p. 391. Thiel, 1936, p. 34.

Two specimens, each about 20 mm in diameter, were taken at slope stations in the eastern and north-eastern approaches to Bass Strait (stations 5 and 10 in Fig. 1). Both were taken in open hauls, 500 m and 750 m respectively to the surface. According to previous workers the species probably has its centre of distribution between 1000 and 2000 m, but a few captures have been made very close to the surface.

H. minimum was first recorded for Australian waters by Kramp, from deep water off Low Isles. It is known from all seas, including the Antarctic and extreme North Pacific and North Atlantic, except the high Arctic Ocean and Mediterranean.

HALISCERA CONICA Vanhöffen

Haliscera conica Vanhöffen, 1902, p. 72, pl. 9, fig. 6, pl. 11, fig. 33; 1912, p. 381.

Halicreas conica Mayer, 1910, p. 394. Bigelow, 1938, p. 121.

Homoeonema conica Kramp, 1924, p. 29.

Halicreas album (partim) Thiel, 1936, p. 37.

One specimen, taken between 300 and 400 m at a station east of Bass Strait (station 1, Fig. 1), belongs to this species. It is 8 mm in diameter, flatter than a hemisphere, with an apical projection; and has eight oval gonads, one in the middle of each broad radial canal, a round mouth, and 64 tentacles. The tentacles are almost all very short, as in Vanhöffen's figure, and are apparently broken, but to judge from the size of the tentacle-bases all were originally of about the same size; one tentacle (not at the base of a radial canal) is about 1.5 mm long, in structure like that figured by Russell (1953, p. 457) for *H. bigelowi* Kramp. No more than one sensory club was noted in any octant of the bell-margin, but the spacing suggested that the number per octant is probably two or three.

This specimen constitutes a new record of the species for the Australian region and for the Pacific. It has previously been found in the Indian Ocean, between 900 and 1800 m; in deep water in the Mediterranean; to the west of the British Isles; and in the South Atlantic and Antarctic. Some of the specimens recorded from other localities by Thiel as *Halicreas album* were possibly this species.

HALITREPHES VALDIVIAE Vanhöffen

Halitrephes valdiviae Vanhöffen, 1912, p. 384. Bigelow, 1938, p. 125.

Three specimens were obtained, one each from three slope stations around Tasmania (stations 7, 11, and 12, Fig. 1). All were very battered, and only on the smallest specimen was it possible to count canals and tentacles with confidence.

This specimen is 18 mm in diameter and has 16 broad radial canals, 32 tentacles, and 16 sensory clubs; most of the tentacles are broken but one is about half as long as the radius of the medusa, resembling tentacles of *Haliscera* in structure; no close relationship is apparent between the sensory clubs and the tentacles or canals, but some of the clubs might not have developed or might have been broken off. On the second specimen, 25 mm in diameter, no traces of canals remain, but the number of tentacles is about 50. The largest, 40 mm in diameter, has traces of two canals in one octant of the bell, and thus probably had 16 canals in life, and about 110 tentacles.

These observations agree fairly well with those of Vanhöffen and Bigelow on other specimens at similar sizes.

One of these specimens was taken in a closing net haul from 800 to 500 m, one in an open haul from 500 m to the surface, and one between 230 m and the surface. These observations confirm those of other workers as to its bathypelagic status.

Previous records were from tropical and subtropical latitudes (32° N. to 34° S.) in the Atlantic and Indian Oceans. The specimens here described extend the known distribution of the species to the Pacific and to the comparatively high latitude of 44° S.

BOTRYNEMA BRUCEI Browne

Botrynema brucei Browne, 1908, p. 239, pl. 1, figs. 8, 9; pl. 2, fig. 1. Mayer, 1910, p. 395. Kramp, 1947, p. 11. Russell, 1953, p. 459.

Alloionema ellinorae Hartlaub, 1909, p. 8.

One very damaged specimen, 17 mm in diameter, was taken between 500 and 2200 m in the eastern approaches to Bass Strait (station 1, Fig. 1). Sufficient remains of one portion of the bell-margin to show that the arrangement of tentacles is that of this species. The apical thickening of the bell is distinct, but large and dome-shaped rather than small and conical; in fact in this respect the specimen resembles *ellinorae*, as figured by Hartlaub, more than *brucei*, and might be referred to the former species if the two were regarded as distinct. Kramp believed that they could be distinguished according to the presence or absence of a conical knob, and differences in colour, but these are not good characters for distinguishing species of medusae.

If this specimen were recognized as *ellinorae* the known distribution of that species would be Arctic and south-east Australian waters, while the known distribution of *brucei* would remain the Antarctic, sub-Antarctic, Atlantic south of lat. 31° S., and North Atlantic and North Pacific Oceans, both species being bathypelagic. It is much more likely that there is only one world-wide species, *brucei*. The centre of distribution, bathymetrically, is probably below 1000 m.

Order **NARCOMEDUSAE**

Family **SOLMARIDAE**

SOLMARIS RHODOLOMA (Brandt)

Aequorea rhodoloma Brandt, 1838, p. 357.

Solmaris rhodoloma Maas, 1909, p. 39, pl. 3, fig. 20. Uchida, 1928, p. 85. Kramp, 1953, p. 302.

Solmaris is represented in these collections by 89 specimens, a larger number than for any other species of Narcomedusae; but 64 of these were taken in two 50-0 m vertical plankton hauls on the same day at the same station, 40 in one haul and 24 in another, and no other haul yielded more than three. One was obtained in shelf waters off the north-east corner of Tasmania, one far offshore (station 2 in Fig. 1), and all the others in shelf waters along the New South Wales coast.

The smallest specimen is 1.3 mm in diameter, the largest 8 mm. Measurements and counts of tentacles for 16 specimens taken at random are as follows:

1 mm 12, 12; 2 mm 12, 15, 16; 3 mm 20; 4 mm 27; 5 mm 24, 31; 6 mm 36; 7 mm 29, 29, 30, 32; 8 mm 34, 36.

These tentacle numbers are very slightly lower than those recorded by Kramp for *S. rhodoloma* at Low Isles, and there can be little doubt that the same species occurs in both regions, i.e. all along the east coast of the Australian mainland. Tentacle counts of Japanese specimens of *S. rhodoloma* by Maas and Uchida also agree closely, as Kramp observed. The differences between this species and *S. corona* (Keferstein & Ehlers) seem small, and Mayer (1910, p. 437) and Thiel (1936, p. 64) were inclined to unite them. Specimens of *S. corona* observed by Browne (1900, p. 733) had slightly fewer tentacles at all sizes than corresponding specimens of *rhodoloma*, and attained a greater size. Possibly the two forms are subspecies of the same species, *rhodoloma*.

Records of *S. rhodoloma* outside Australia are available from Japan (lat. 35° N.), Chile (about lat. 37° S.), and the Pelew Islands in the tropical Pacific. If *S. corona* were included the range of the species would also cover the North and central Atlantic, the Mediterranean, and possibly the Indian Ocean (Russell 1953, p. 478). Both species are epipelagic.

Family AEGINIDAE

AEGINA CITREA Eschscholtz

Aegina citrea Eschscholtz, 1829, p. 113. Mayer, 1910, p. 451, figs. 299, 300. Bigelow, 1938, p. 131. Russell, 1953, p. 467.

Aegina rosea Eschscholtz, 1829, p. 115. Thiel, 1936, p. 73.

It is now generally agreed (Thiel, Bigelow, Russell) that only one good species, which must bear the earliest name *citrea*, can be recognized. This species has been taken at several localities in shelf waters of Queensland and New South Wales from lat. 27° S. to 37° S., and up to 100 miles offshore in this region. It is not common there, only about 20 specimens having been seen. Some of these are pentamerous. The greatest depth from which any of these specimens could have come was 146 m. Records by other authors show that this species is more eurybathic than any other described previously in this paper, except possibly *Sminthea eurygaster*: although repeatedly found at the surface it has also been taken several times in closing nets at considerable depths, as far down as 900-1100 m.

Although not previously recorded from Australian waters, the species has been taken in many parts of the world, including the three oceans and the Mediterranean, from lat. 63° N. to the Antarctic. The Antarctic record is that of *Aegina* sp. by Vanhöffen (1912, p. 388).

SOLMUNDELLA BITENTACULATA (Quoy & Gaimard)

Charybdea bitentaculata Quoy & Gaimard, 1833, p. 295.

Solmundella bitentaculata Mayer, 1910, p. 455, pl. 54, figs. 1-3; pl. 55, fig. 4. Thiel, 1936, p. 68. Kramp, 1953, p. 302.

The distribution of this species in the south-east Australian region is in shelf and inner slope waters as far south as lat. 41° S., excluding Bass Strait and its western approaches. It has not been found far offshore. Only 31 specimens were obtained, up to 10 in a single bottom-to-surface haul in shelf waters. All are small, corresponding to variety *mediterranea* (Müller); the diameter of one of the largest is only 4 mm and its tentacles are 10 mm long.

According to other authors the vertical range of this species is wide, like that of *Aegina citrea*; it has been repeatedly taken at various depths from the surface to between 900 and 1100 m.

Solmundella has been recorded twice previously from Australian waters: from Torres Strait (Mayer 1915, as *S. mediterranea*) and Low Isles (Kramp). It is widely distributed in the three oceans, as far north as the Sea of Ochotsk and as far south as Antarctica, and occurs in the Mediterranean.

Family CUNINIDAE

CUNINA OCTONARIA McCrady

Cunina octonaria McCrady, 1857, p. 109, pl. 12, figs. 4, 5. Kramp, 1953, p. 304.

Cunoctantha octonaria Mayer, 1910, p. 461. Thiel, 1936, p. 82.

Ten specimens were obtained from shelf and adjacent slope waters, from the central coast of New South Wales through Bass Strait (southern part only) to the western approaches. It has not been found far offshore. Those taken in Bass Strait and further west were the only representatives of their order to be found there.

These medusae range from 2 to 5 mm in diameter; the number of tentacles is eight in eight specimens and 11 (but only 10 stomach pouches, two tentacles arising together in the radius of a single pouch) in two specimens. Kramp has drawn attention to similar variations. In other respects all specimens were typical of this species.

The single specimen from the continental slope was taken between 50 and 100 m. Thiel also recorded captures at this depth, and closer to the surface, but there appears to be no record of its occurrence below 100 m.

Kramp recorded this species from Low Isles. It occurs in all three oceans between about lat. 40° N. and 40° S., and in the Mediterranean.

CUNINA RUBIGINOSA (Kölliker)

Eurystoma rubiginosum Kölliker, 1853, p. 322.
Cunina rubiginosa Kramp, 1924, p. 37. Thiel (partim), 1936, p. 77.
Cunina prolifera Mayer, 1910, p. 480, figs. 319, 320.
?*Cunina prolifera* Gegenbaur, 1854, p. 56.

Five specimens were obtained, all from the uppermost 50 m of water: one at a shelf station in lat. 25° S., three at a shelf station in lat. 33° S., and one at a slope station east of Bass Strait (station 1, Fig. 1).

Diameters and tentacle numbers are as follows: 4 mm, 11 tentacles; 5 mm, 8 and 11; 8 mm, 9; 9 mm, 14. The stomach pouches are mere notches in the stomach-margins, and other features likewise agree with those of *C. rubiginosa*.

All specimens were obtained from the uppermost 50 m of the sea. According to other authors the species is epipelagic in the young stages at least; it has been suggested (Thiel) that it sinks to much greater depths as it grows larger, but it is not certain that these larger individuals belong to the same species. The geographical distribution is likewise uncertain because of doubts as to which if any of the other described species of *Cunina* should be referred to *C. rubiginosa*. Positive records exist only for the Mediterranean and the warmer waters (lat. 31° N. to 48° N.) of the North Atlantic; but Thiel, who includes several other species in the synonymy, records it in the warmer parts of all three oceans. None of these forms has previously been found in the Australian region.

CUNINA DUPLICATA Maas

Cunina duplicata Maas, 1893, p. 52, pl. 5, figs. 9, 10. Mayer, 1910, p. 481.

Three specimens from the uppermost 100 m of water, two from shelf and one from slope waters off the New South Wales coast between lat.

31° S. and 33° S., are referable to this species, which has not been recorded since it was originally described from a single specimen taken in deep water in the tropical Atlantic. Each measures 6-7 mm in diameter and has 16 tentacles, eight long alternating with eight short, and 16 well-defined stomach pouches of which those corresponding to the shorter tentacles are narrower than the other eight. These features distinguish the specimens sharply from those of *C. rubiginosa*, even from specimens of similar size taken in the same haul, which they resemble in other respects.

There is, however, a considerable variation in the size of the tentacles of the two sets. Approximate lengths in terms of bell radius *r*, which for all three specimens is about 3 mm, are given for each specimen as follows:

No.	Long series	Short series
1	0.5 *r*	0.1 *r*
2	1.0 *r*	0.2-0.5 *r*
3	1.2 *r*	0.2-0.6 *r*

In Maas's specimen of radius 10 mm, the long tentacles were about twice as long as the short and probably only about half the radius of the bell.

SOLMISSUS MARSHALLI Agassiz & Mayer

Solmissus marshalli Agassiz & Mayer, 1902, p. 151; pl. 5, figs. 23-25. Mayer, 1910, p. 484. Bigelow, 1919, p. 329. Thiel, 1936, fig. 13.

Seven specimens of *Solmissus* were taken, one from a shelf station on the northern part of the New South Wales coast, five from slope stations up to 150 miles offshore between lat. 25° S. and 37° S., and one from a slope station off eastern Tasmania (station 7, Fig. 1). It was not found in Bass Strait or further west.

All specimens were in poor condition and one was incomplete. The diameters and tentacle counts for the other six are: 10 mm, 14 tentacles; 14 mm, 16; 20 mm, 10; 25 mm, 10; 30 mm, 13; 35 mm, 12. The stomach pouches are markedly rectangular and the number of sensory clubs per lappet, although not determinable with certainty in any part of any specimen, was clearly of the order of 7-12. Identification with *S. marshalli* can thus be made with certainty.

One specimen was taken between 100 and 200 m, the others all from closer to the surface. Previous records likewise have been mainly from the upper layers. The species is probably epipelagic. It has not been recorded from the Australian region before, although it is widespread in the warm waters of the Pacific and has been found in the warmer parts of the Atlantic and Indian Oceans, approximately between lat. 35° N. and 35° S.

III. DISCUSSION

The 20 species noted above for south-east Australian waters may be divided, according to their vertical distribution in Australian waters and elsewhere, into three groups.

The first includes those species which are clearly epipelagic, seldom found more than 200 m below the surface: *Geryonia proboscidalis, Liriope tetraphylla, Rhopalonema velatum, Aglaura hemistoma, Solmaris rhodoloma, Cunina octonaria,* and probably *Cunina rubiginosa* and *Solmissus marshalli.*

The second group comprises the characteristically bathypelagic species, commonest below 200 m: *Colobonema sericeum, Pantochogon haeckeli, Aglantha elongata, Halicreas minimum, Haliscera conica, Halitrephes valdiviae,* and *Botrynema brucei,* all of which are Trachymedusae.

The third group is needed for the reception of five species which cannot conveniently be placed in the other two groups, and which it would at present be more correct to describe as probably eurybathic in the uppermost 1000 m: *Sminthea eurygaster, Persa incolorata, Aegina citrea, Solmundella bitentaculata,* and *Cunina duplicata.*

As would be expected, the second and third groups contain a higher proportion of cosmopolitan species than does the first. *Pantochogon* and *Botrynema* occur in the Arctic and Antarctic regions as well as in intermediate latitudes; *Halicreas, Haliscera, Aegina,* and *Solmundella* occur from the cool-temperate waters of the northern hemisphere to the Antarctic; *Colobonema* occurs from lat. 65° N. to 42° S.; and *Sminthea* is found between lat. 50° N. and 57° S.* The other species, as far as known at present, are restricted to lower latitudes, although even the little-known *Cunina duplicata* ranges from lat. 10° N. in the Atlantic to 30° S. in the Pacific. All species in these groups have now been recorded from the Atlantic and Pacific Oceans, and most of them from the Indian Ocean as well. *Botrynema* has not been recorded from the tropics but probably occurs there at great depths in very cold waters.

The epipelagic species are as a group more localized geographically, in a way that warrants examination of the possibility of using them as indicators of water masses. Although at least six and possibly all eight† of them occur in all three oceans, and all occur from time to time in neritic as well as oceanic waters, their ranges in latitude are narrower than those of most of the species discussed above. This is shown in Table 1, which also includes particulars of *Amphogona apsteini* (Vanhöffen), another epipelagic Trachymedusa which has been recorded from

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* *Aeginura,* another bathypelagic form which occurs in the Australian region although not seen in these investigations (see Section I), is also widely distributed; it ranges from lat. 64° N. to 47° S. (Thiel 1936, p. 88).

† The two doubtful species are *Cunina rubiginosa,* which probably occurs in the Indian Ocean as it does in the other two; and *Solmaris rhodoloma,* a Pacific form which may be identical with the more widespread *S. corona.*

Australia although not in these investigations (Kramp 1953, Low Isles; see Section I).

There is, therefore, in south-east Australian waters a gradual decline in the number of epipelagic species from lower to higher latitudes, some dropping out of the fauna and no others coming in. The change in the fauna with latitude is actually even more marked than Table 1 would suggest, as both *Aglaura* and *Rhopalonema*, the former particularly, become increasingly rare south of lat. 39° S. Any evidence of large numbers of these species south of 39° S. would suggest unusual environmental conditions. However, the only species which promises to be of constant value as an indicator of hydrological conditions in this region is *Liriope tetraphylla*, which is moderately abundant and widespread in waters as far south as 39° S. but has so far not been seen at all further south; it may be confined to the northern of the two major water masses which are believed to exist off the south-east Australian coast.

TABLE 1

KNOWN LATITUDE LIMITS OF AUSTRALIAN EPIPELAGIC MEDUSAE

Species	World Range incl. Australia	S. Limit in E. Australia
Amphogona apsteini	34° N.-16° S.	16° S.
Geryonia proboscidalis	35° N.-35° S.	25° S.
Liriope tetraphylla	50° N.-39° S.	39° S.
Cunina rubiginosa	48° N.-39° S.	39° S.
Solmaris rhodoloma	35° N.-41° S.	41° S.
Cunina octonaria	43° N.-41° S.	41° S.
Solmissus marshalli	34° N.-43° S.	43° S.
Aglaura hemistoma	45° N.-43° S.	43° S.
Rhopalonema velatum	58° N.-49° S.	44° S.

It is interesting that only two species, *Aglaura hemistoma* and *Cunina octonaria*, occur in the central part of Bass Strait; much more plankton collecting has been done in this area than in the eastern and western approaches to the Strait, where the following additional species were collected in the upper layers: *Rhopalonema velatum* (east and west), *Sminthea eurygaster* (east and west), *Solmaris rhodoloma* (east only), *Solmundella bitentaculata* (east only), and *Cunina rubiginosa* (east only).* On the facts available it is impossible to decide whether *Aglaura* and *Cunina octonaria* are endemic or exotic species as far as Bass Strait is concerned. So far they have only been found in that region (only in the southern part; see Fig. 1) in the autumn, at a time when *Aglaura* is present in both the eastern and western approaches and *Cunina* in the western approaches; more collecting has been done in the western than in the eastern approaches in the autumn months.

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* *Solmissus marshalli* probably also occurs in the eastern approaches, since it occurs both north and south of that region.

IV. ACKNOWLEDGMENTS

Thanks are due to Dr. H. Herdman of the Discovery Committee, London, for arranging for medusae to be collected by R.R.S. *Discovery II* in Australian waters in October 1950, sorted, and made available to the Division of Fisheries, C.S.I.R.O.; and to Mr. R. Breach of the Division of Fisheries for preparation of the figure.

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THE ZOOPLANKTON OF LAKE MACQUARIE, 1953-1954

By PATRICIA KOTT*

(*Manuscript received March* 8, 1955)

Summary

A quantitative account of the faunal succession in Lake Macquarie, N.S.W., from June 1953 to July 1954 is given. Comparisons are made between the zooplankton of the lake and those of the neighbouring sea and estuaries. It is concluded that the level of zooplankton of Lake Macquarie is well below that of the coast and that it is a specialized and relict marine fauna rather than an estuarine fauna.

I. INTRODUCTION

Collections in the lake were planned to show:

(*a*) The relationships of lake zooplankton to the zooplankton of coastal waters outside the lake and of the estuaries along the neighbouring coast.

Jibbon, an onshore station 60 miles south of the Lake Macquarie entrance, and Port Stephens, 35 miles to the north, have been compared to indicate the probable composition of zooplankton outside the lake.

(*b*) The successions of species throughout the year in the lake; and regional and temporal variations in quantitative and qualitative populations which might indicate water movements or productivity within the lake.

The work was planned to continue over several years but unfortunately circumstances forced it to be terminated after July 1954. It is hoped that the work may continue, particularly in regard to the low level of zooplankton observed in the lake, the cause and form of successive peaks of certain species, invasions from onshore plankton, diurnal migration, and relationships of phytoplankton and zooplankton.

II. ENVIRONMENT

Lake Macquarie is a partially enclosed salt-water lake, with a narrow entrance to the sea extending for about 2 miles (Fig. 1). It is about 12 miles long with a maximum depth of 12 m. The two main freshwater creeks into the lake are Dora Creek in the south and Cockle Creek in the north. These do not, however, cause any appreciable variations in the salinity of the lake except in times of flood (Rochford 1955). Other physical characters of the water are essentially marine (Rochford 1955). However, whereas the temperature of the water in the sea remains constant throughout the day and varies annually between 16° and 23°C, the lake waters have a diurnal range of up to 2°C and the annual range is from 11° to 24°C. The tidal flow in the entrance to the lake is strong

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but the influence of the tide extends only to the stations around the entrance. The "tidal range" is only a few inches.

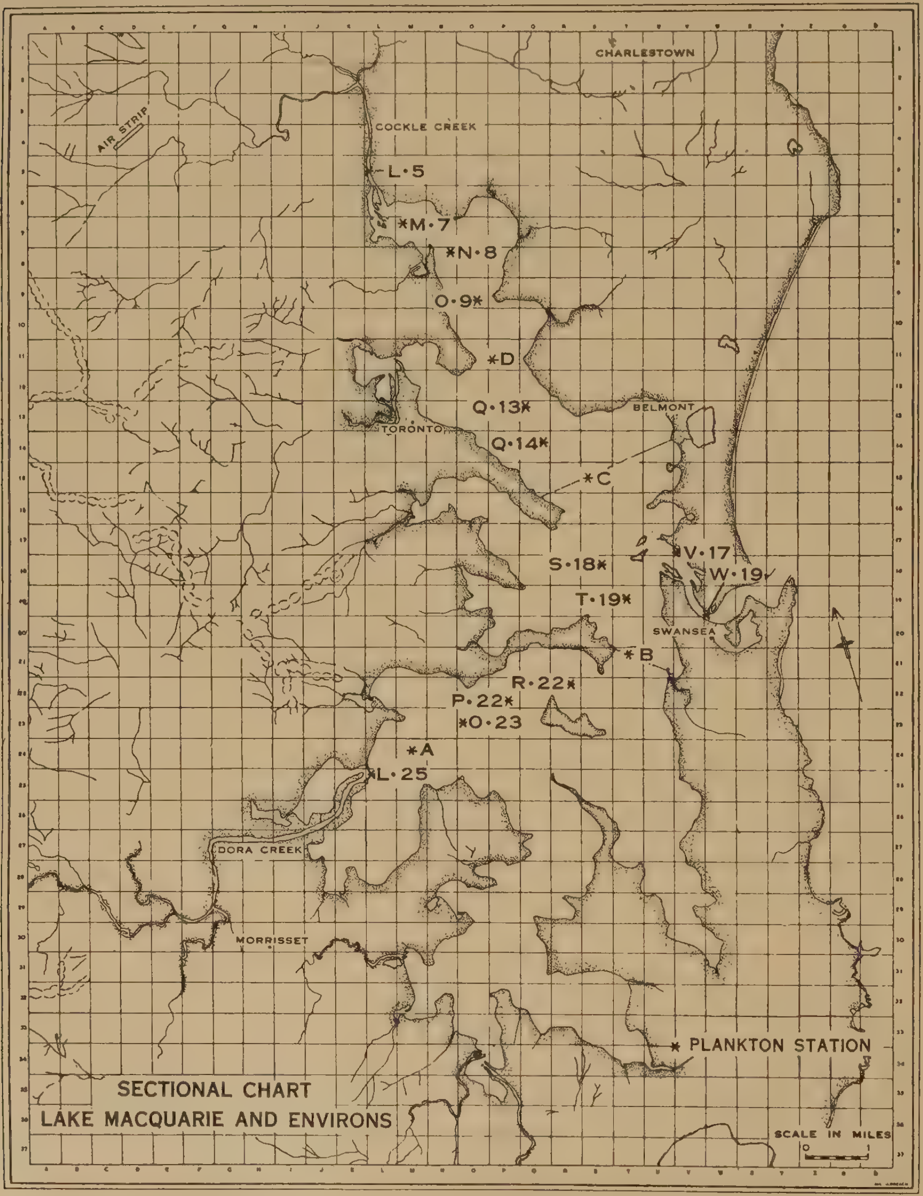
CHARLESTOWN
AIR STRIP
COCKLE CREEK
L·5
M·7
N·8
O·9
D
Q·13
TORONTO
BELMONT
Q·14
C
V·17
S·18
W·19
T·19
SWANSEA
B
R·22
P·22
O·23
A
L·25
DORA CREEK
MORRISSET
PLANKTON STATION
SECTIONAL CHART
LAKE MACQUARIE AND ENVIRONS
SCALE IN MILES
0
1

Fig. 1.—Map of Lake Macquarie showing stations.

III. Methods of Collection

The nets used in the lake were, initially:

(*a*) Discovery type N70.

(*b*) A modified type of N70 with mouth diameter half that of the Discovery N70 and exclusively 74 mesh/in. silk. Both these nets were protected by mesh across the mouth to prevent their being fouled by the jelly-fish *Aurelia coerulea* R. von Lendenfeld, which is particularly plentiful in the lake.

(*c*) Clarke-Bumpus closing net with flowmeter (Clarke and Bumpus 1950).

Hauls were taken simultaneously with all nets to test their efficiency. The two smaller nets were more easily handled and took the more efficient sample (often greater than the N70, despite the fact that the mouth diameter of the latter is five times that of the Clarke-Bumpus net). This may partially be accounted for by the loss of catch through the larger meshes around the mouth of the N70; by the difficulties of hand-hauling the large net from a small boat; and by the fact that the flowmeter mechanism, encased in a metal cylinder at the mouth of the Clarke-Bumpus, provides an effective barrier to the escape of the catch over the mouth of the net.

Both the smaller nets were used subsequently. All data have been adjusted to represent the fauna filtered from 400 l. of water, i.e. the amount of water filtered by the Clarke-Bumpus net towed for 7 min at 1.5 knots. Hauls were taken once a month for the 13 months of the survey. Unfortunately no continuous survey could be maintained at any one station for direct observations on diurnal variations and vertical migration. All hauls were taken during daylight hours. Stations sampled (L.5 to L.25) are shown in the map (Fig. 1); at all stations horizontal hauls were taken at the surface and at the deeper stations horizontal hauls were taken within 0.5 m of the bottom. Data for the coastal stations were extracted from plankton records of the Division of Fisheries, C.S.I.R.O. (Kott 1954).

Information on estuarine plankton has been obtained from the work of Miss M. Morris, Macleay Fellow of the Linnean Society of New South Wales, in 1949, on the zooplankton of the Hawkesbury estuary. The full report of this work is available in the Fisher Library of the University of Sydney, and there is a published summary (Rochford 1951). Supplementary data from other coastal estuaries were obtained from occasional collections made by the Division of Fisheries in the Port Hacking and Georges River estuaries in 1945 and 1946, in conjunction with hydrological sampling (Rochford 1952).

Species have been identified from Dakin and Colefax (1940), Henry (1919), and Nicholls (1945).

IV. RESULTS

The results of the survey are summarized in Tables 1 and 2 and in Figures 2-5.

Larval forms and eggs occur in the lake as follows: lamellibranch larvae—from October to May with a peak in February; decapod larvae—throughout the year, but in decreased numbers from February to July, with a general peak throughout the lake in December and a localized peak at the south end of the lake near Dora Creek in August.

TABLE 1

MAXIMUM NUMBERS OF SPECIES WHICH MAY OCCUR AT ANY TIME, INDICATING THE RELATIVE IMPORTANCE* OF SPECIES IN THE THREE SYSTEMS

×××××, Dominant; ××××, dominant in lake or estuaries, seasonal dominance in the sea; ×××, subdominant or seasonal; ××, fair numbers only; ×, rare occurrence

Species	Lake Macquarie	Estuaries	Coastal Marine	
			Jibbon	Port Stephens
Copepods				
Temora turbinata	××	×××	×××××	×××××
Acartia clausii	××××	××××	×××××	×××××
Calanoides brevicornis	×	—	××××	××××
Undinula spp.	—	—	×××	×××
Centropages spp.	—	—	××	××
Tortanus barbatus	×××	×	—	—
Gladioferens spp.	××	×××	—	—
Pseudodiaptomus spp.	×	××	—	—
Sulcanus conflictus	—	××	—	—
Cladocera				
Penilia schmackeri	××	××	×××××	×××××
Evadne tergestina	××	×××	×××××	×××××
Evadne spinifera	×	—	×××	×××
Evadne nordmanni	×××	—	—	××
Podon polyphemoides	×××	×××	××	×
Appendicularia				
Oikopleura longicauda	—	—	×××	×××
Oikopleura rufescens	×	—	××	××
Oikopleura fusiformis	—	—	××	××
Oikopleura dioica	××	××	—	—
Acopa				
Thalia democratica	—	—	×××××	××××
Doliolum denticulatum	×	—	×××	×××
Chaetognaths				
Sagitta enflata	×	—	××	××
Sagitta neglecta	×××	×××	××	××
Coelenterata				
Aurelia coerulaea	×××	×××	—	—

* *Paracalanus* spp. are ubiquitous in these environments and are not included in the tables.

Fish eggs and larvae (particularly eggs of the anchovy, *Engraulis australis* (Shaw)) were plentiful in October, especially at the north end

TABLE 2

ANNUAL VARIATIONS IN ZOOPLANKTON IN LAKE MACQUARIE AND IN COASTAL WATERS

<table>
<tr><th rowspan="2">Species</th><th rowspan="2">Lake Macquarie</th><th colspan="2">Coastal Marine</th></tr>
<tr><th>Port Stephens</th><th>Jibbon</th></tr>
<tr><td>Copepods</td><td></td><td></td><td></td></tr>
<tr><td><i>Temora turbinata</i></td><td>Through year</td><td>Absent: Aug., Sept.
Peak: March</td><td>Through year
Peak: Jan.-Apr.</td></tr>
<tr><td><i>Acartia clausii</i></td><td>Through year</td><td colspan="2">Absent: Aug., Sept.
Peak: Mar.-May</td></tr>
<tr><td><i>Calanoides brevicornis</i></td><td>Mar.</td><td colspan="2">Sept.-Oct.</td></tr>
<tr><td><i>Undinula</i> spp.</td><td>—</td><td colspan="2">Jan.-Aug.</td></tr>
<tr><td><i>Tortanus barbatus</i></td><td>Oct.-July
Peak: Dec., Jan.</td><td colspan="2">—</td></tr>
<tr><td><i>Gladioferens</i> spp.</td><td>July-Oct., Apr.-June
Peak: Aug.</td><td colspan="2">—</td></tr>
<tr><td><i>Pseudodiaptomus</i> spp.</td><td>Nov.</td><td colspan="2">—</td></tr>
<tr><td><i>Sulcanus conflictus</i></td><td>—</td><td colspan="2">—</td></tr>
<tr><td>Cladocera</td><td></td><td></td><td></td></tr>
<tr><td><i>Penilia schmackeri</i></td><td>Nov.-Jan., Mar., May
Peak: Nov.</td><td>Through year
Peak: Mar., Apr.</td><td>Absent: Sept., Nov.
Peak: Apr.</td></tr>
<tr><td><i>Evadne tergestina</i></td><td>Oct.-Mar.
Peak: Nov.</td><td>June-May
Peak: Sept.</td><td>Nov.-May
Peak: Jan.</td></tr>
<tr><td><i>Evadne spinifera</i></td><td>Nov.-Feb.</td><td>Absent: Feb., Mar.
Peak: Sept.-Oct.</td><td>Apr., June, Nov.</td></tr>
<tr><td><i>Evadne nordmanni</i></td><td>June-Nov.
Peak: Aug.</td><td>Dec.</td><td>—</td></tr>
<tr><td><i>Podon polyphemoides</i></td><td>June-Dec.
Peak: Aug.</td><td>Sept.-Jan.</td><td>Aug.-Nov.</td></tr>
<tr><td>Appendicularia</td><td></td><td></td><td></td></tr>
<tr><td><i>Oikopleura longicauda</i></td><td>—</td><td colspan="2">Through year</td></tr>
<tr><td><i>Oikopleura rufescens</i></td><td>Mar.</td><td colspan="2">Sept., Mar.</td></tr>
<tr><td><i>Oikopleura fusiformis</i></td><td>Mar.</td><td colspan="2">Through year</td></tr>
<tr><td><i>Oikopleura dioica</i></td><td>June-Nov.
Peak: Nov.</td><td colspan="2">—</td></tr>
<tr><td>Acopa</td><td></td><td></td><td></td></tr>
<tr><td><i>Thalia democratica</i></td><td>—</td><td colspan="2">Mar., Sept.</td></tr>
<tr><td><i>Doliolum denticulatum</i></td><td>Mar.</td><td colspan="2">Absent: Oct.-Feb.</td></tr>
<tr><td></td><td></td><td>Peak: Sept.</td><td>Peak: Mar.</td></tr>
<tr><td>Chaetognaths</td><td></td><td></td><td></td></tr>
<tr><td><i>Sagitta enflata</i></td><td>Mar.</td><td colspan="2">Through year</td></tr>
<tr><td><i>Sagitta neglecta</i></td><td>Absent: Sept.
Peak: Jan.</td><td colspan="2">Through year</td></tr>
<tr><td>Coelenterata</td><td></td><td></td><td></td></tr>
<tr><td><i>Aurelia coerulaea</i></td><td>Through year</td><td></td><td></td></tr>
</table>

of the lake, and persisted until December. The numbers then decreased from January through February and March, and became negligible after April.

V. Discussion

(*a*) *Coastal Zooplankton*

From Tables 1 and 2 it is evident that there are only small differences between the zooplankton of the Port Stephens and Jibbon areas. Port Stephens, as the closest marine station, has therefore been considered as representative of the conditions outside Lake Macquarie.

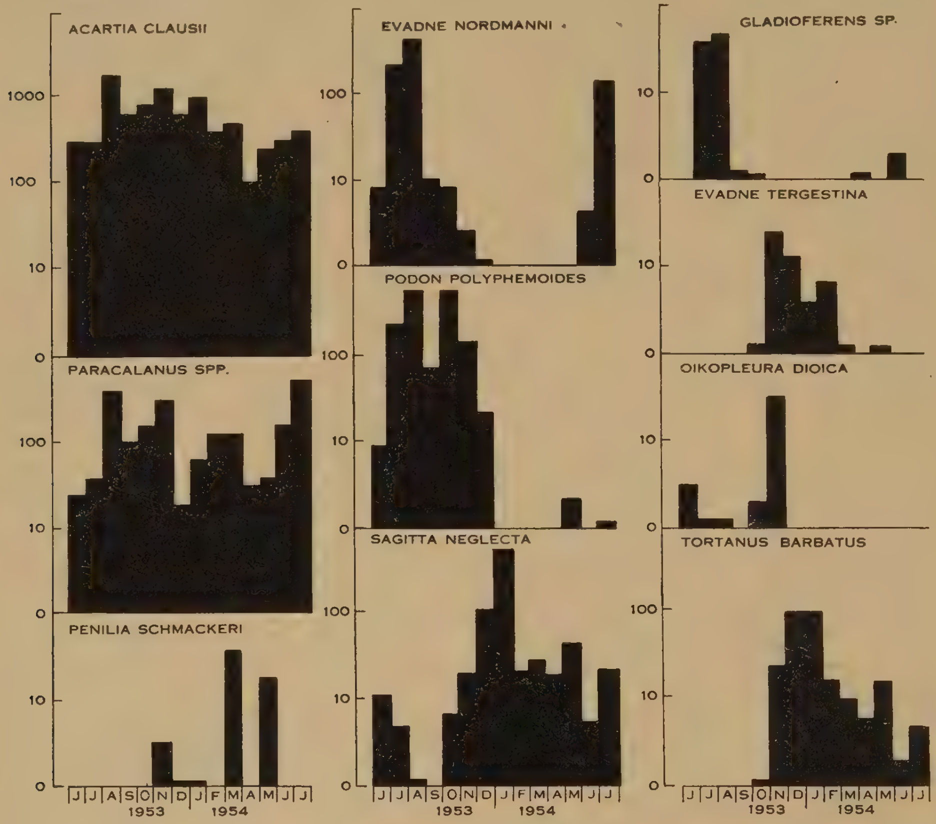

Fig. 2.—Average numbers of each species from 400 l. of lake water at 10-15 stations throughout the lake from June 1953 to July 1954; plotted logarithmically.

(*b*) *Estuarine Zooplankton*

Pseudodiaptomus spp. typical of the freshwater end of an estuarine system have been recorded from May to September at the ballast heap in the Port Hacking estuary, in association with *Tortanus barbatus* (Brady), *Temora turbinata* (Dana), *Paracalanus* spp., and *Evadne tergestina* Claus, and from June to December at Milperra in the Georges River with *Gladioferens* spp.; in the Hawkesbury River estuary it was common as far down the river as station 15 (Rochford 1951; 1952, Vol. 5), in association with *Gladioferens* spp. and *Sulcanus conflctus* Nicholls. *Sulcanus conflctus*, a "typical" conflict zone species (Nicholls 1945), was taken from the Georges River at Tom Ugly's Point in May and June 1945. *Tortanus barbatus* has not been recorded from the Georges River, nor from the Hawkesbury River. With these two exceptions all species listed in Table 1 as present in estuaries are common to the three estuaries discussed above.

(*c*) *Lake Macquarie Zooplankton*

The zooplankton of Lake Macquarie is grouped for discussion in several different ways as follows:

(i) Order of dominance in the lake.
(ii) Seasonal succession in the lake, in relation to coastal succession.
(iii) Relation to the zooplankton communities of other environments.
(iv) Total zooplankton.
(v) Vertical migration.

(i) *Order of Dominance in the Lake.*—The species found throughout the year were *Acartia clausii* Giesbrecht, *Paracalanus parvus* (Claus), *Temora turbinata*, *Sagitta neglecta* Aida, and *Aurelia coerulea* R. von Lendenfeld.

There were seasonal occurrences, persisting for several months, of *Evadne nordmanni* Loven, *Podon polyphemoides* Leuck, *Tortanus barbatus*, *Gladioferens brevicornis* Henry, *Oikopleura dioica* Fol, *Evadne tergestina*, *Penilia schmackeri* Richard, *Beroe* sp., and *Phyllorhiza punctata* von Lendenfeld.

Also in March 1954, the following appeared in small numbers and for a short period at a few stations near the entrance: *Doliolum denticulatum* (Quoy & Gaimard), *Oikopleura rufescens* Fol, and *Sagitta enflata* Grassi.

Small numbers of *Evadne spinifera* Muller also occurred from November to March; and *Proboscidactyla ornata* (McCrady) was present in November in the entrance channel.

(ii) *Seasonal Succession.* (1) *Species Present Throughout the Year.*—*Acartia clausii* was dominant for most of the year and reached its peak in August. *Paracalanus* spp. were also present in large numbers, increasing particularly in July when this genus exceeded the numbers of *Acartia*. These species dominate not only the lake but also the fauna of the other environments under discussion. Their dominance in the lake is, however, more prolonged than in the sea and in the estuaries, where to a large extent they are replaced by *Temora turbinata* for part of the year. *Temora turbinata* was present in the lake throughout the year, but never in the large numbers which occur in coastal and estuarine waters. *Aurelia coerulea* is a component of estuarine zooplankton which was always present in the lake. In June 1953 the lake was fouled with a brown slime identified as decomposing *Aurelia*; in the following month the population was regenerated by the appearance of many small specimens. *Sagitta neglecta* was always present and increased to huge numbers from October to January. It is present in similarly large numbers in estuaries but in much smaller numbers in the marine plankton.

(2) *"Winter Species"*.—From June to August *Evadne nordmanni, Podon polyphemoides*, and *Gladioferens brevicornis* gained a general distribution over most of the lake. *Evadne nordmanni* is plentiful here. It is also the common cladoceran in the plankton off Eden, N.S.W., and south of Eden in the Bass Strait. It has, however, occurred occasionally further north—in small numbers off Jibbon in March 1945, February 1947, October and December 1949, and December 1953, and off Port Macquarie in January 1950 and December 1953. It is therefore not a normal component of local marine onshore zooplankton, nor has it been taken in the estuaries (*Evadne tergestina* is the cladoceran present in the sea and in the three estuaries at present under consideration). When this species occurred off Jibbon in 1953, it had already disappeared from Lake Macquarie. Therefore, its presence here is not apparently related to the marine population.

Podon polyphemoides was present from June to December and reappeared again the following May. Its occurrence in the lake therefore overlaps with its presence in the coastal fauna (September-January). However, it began to flourish in the lake long before it appeared in the outside waters, and its cycle must be considered an independent one. It is present but not common in estuarine plankton.

Gladioferens brevicornis originated near the entrance of Dora Creek into the lake. From there it spread and was taken in considerable numbers at all stations in August and September. Later appearances in February, April, and June were limited to the stations near Dora Creek. This species does not occur in the marine plankton but is common in estuarine plankton.

(3) *"Spring Species"*.—With the reduced numbers of *Evadne nordmanni* and *Podon polyphemoides* in October, *Oikopleura dioica, Evadne tergestina*, and *Tortanus barbatus* appeared. The two former species rose to a peak in November and quickly disappeared again. *Tortanus barbatus* had a more prolonged cycle in the lake and was still present in considerable numbers in the following July. *Oikopleura dioica* is found mainly in the estuaries and only occasionally in the marine plankton. *Evadne tergestina* is the principal cladoceran of the coastal and estuarine zooplankton and its appearance in the lake in October suggests that this may be related to the peak of the species at Port Stephens in September. It has, however, a very much shorter cycle in the lake than in neighbouring marine waters, and if its appearance in Lake Macquarie is due to a marine influence, this influence is short-lived. There was another occurrence of the species in the lake in May which may have been due to an invasion from outside. The distribution of *Tortanus barbatus* is similar to that of *Evadne nordmanni*; it is common off Lakes Entrance, Vic., and Eden from March to June, made a short appearance off Port Phillip heads in February to May 1951, but does not extend further north in the coastal plankton. It does, however, appear in the Port Hacking estuary (ballast heap, May-July 1946), although it has not been reported from the Hawkesbury River nor

from the Georges River. The absence of this species from the lake in June 1953 (whereas in June 1954 it was present in appreciable numbers) may be due to a heavy influx of fresh water in May 1953.

(4) *"Summer" Species.*—*Penilia schmackeri* appeared in Lake Macquarie in considerable numbers in November. At that time it was absent from the coastal zooplankton. It persisted in the lake until January in gradually decreasing numbers; at the same time the numbers were increasing in the coastal waters and the peak of the species there could possibly account for its sporadic appearance in the lake in March and May. This is a common estuarine species. *Evadne spinifera* was present in small numbers from November to February. The species flourished in the Port Stephens plankton from August to September, reached its peak in October, and disappeared from these waters in March. During these months it apparently invades the lake in small numbers. The species has not been reported from estuarine waters.

(5) *Other Species.*—*Doliolum denticulatum*, *Oikopleura rufescens*, and *Sagitta enflata* only appeared at stations near the entrance channel in small numbers during March, when they were present in large numbers in the onshore plankton. *Undinula vulgaris* (Dana), *Undinula darwinii* (Lubbock), *Oikopleura fusiformis* Fol, *Thalia democratica* Forskål, and *Calanoides brevicornis* (Lubbock) were never present in the lake although common marine species at certain times of the year. *Pseudodiaptomus* spp. were limited to isolated appearances at station M.7, off Mark's Point in November, and in Dora Creek in July 1954. *Sulcanus conflictus*, a typical "conflict zone" copepod (Nicholls 1945), does not ever occur in Lake Macquarie. Nicholls has indicated that it occurs in estuaries all around Australia and its absence from Lake Macquarie may indicate the late origin of this lake.

(iii) *Relation to the Zooplankton Communities of Other Environments.*—(1) Species whose occasional appearance in the lake is apparently related to their presence in the onshore marine fauna: *Oikopleura rufescens*, *Doliolum denticulatum*, and *Sagitta enflata* in March, *Evadne spinifera* in November, January, and February, *Penilia schmackeri* in March and May, and *Centropages furcatus* and *Evadne tergestina* in May.

(2) Species which appear in other estuarine systems (these may also occur in the marine environment but here have a different cycle and relative order of magnitude): *Acartia clausii*, *Temora turbinata*, *Paracalanus parvus*, *Podon polyphemoides*, *Evadne tergestina*, *Penilia schmackeri* (Nov.-Jan.), *Gladioferens* sp., *Sagitta neglecta*, *Aurelia coerulea*, *Oikopleura dioica*, and *Beroe* sp.

(3) Species which occur in the lake in considerable numbers and do not occur in the outside plankton nor usually in estuarine systems: *Evadne nordmanni* and *Tortanus barbatus*.

In August 1953, when the rise in salinity commenced in the lake, the Port Stephens plankton consisted of large numbers of *Thalia democratica, Calanoides brevicornis, Evadne spinifera, Evadne tergestina,* and *Undinula darwinii.* None of these species were present in the lake plankton in August, although in September *Evadne tergestina* did appear.

In March, when there is the greatest apparent invasion of outside plankton into the lake, only *Oikopleura rufescens, Doliolum denticulatum, Sagitta enflata,* and *Penilia schmackeri* were present in the lake to indicate this invasion. Of these species only *Penilia schmackeri* may be a normal component of lake plankton from November to January.

In March *Oikopleura rufescens, Doliolum denticulatum, Penilia schmackeri,* and *Sagitta enflata* were present at station V.17 in the entrance channel and *Doliolum denticulatum* appeared again at station T.19 just south of the entrance. There is therefore a mixing of marine and lake fauna in the entrance channel. Similarly in May, *Penilia* was present at stations M.24 and D in small numbers, *Centropages furcatus* at station T.19, and *Evadne tergestina* at stations C and D (cf. Fig. 1). The coastal marine plankton had the same constituents as it had in March.

In November, January, and February, when *Evadne spinifera* was present in outside waters, it was present in the lake only at stations S.18, V.17, and Q.14.

Therefore, species present in the outside plankton are generally excluded from entry into the lake, but those few which do intrude as a result of the mixing of outside and lake waters, do not gain any general distribution over the lake (except *Evadne tergestina,* which may originally have been introduced from coastal waters in October).

The succession of zooplankton in Lake Macquarie may therefore be considered as now independent of coastal waters.

Nor is the lake typically estuarine in the character of the zooplankton. Quite apart from the species which occur only in the lake, *Temora turbinata, Evadne tergestina, Penilia schmackeri,* and *Gladioferens* sp. all have a different order of magnitude in Lake Macquarie from that in the closest estuaries along the coast. The behaviour of these species in the estuaries and in the sea are more closely related than their behaviour in the lake.

(iv) *Total Zooplankton.*—Total plankton (Fig. 3) in the lake was greatest in August owing to the immense peaks of *Acartia clausii, Evadne nordmanni,** *Podon polyphemoides,* and *Gladioferens brevicornis.* There was a smaller peak in November owing to the increase in *Oikopleura dioica, Evadne tergestina, Tortanus barbatus,* and *Sagitta neglecta.* There was then a decrease until April, followed by a gradual increase until the conditions of the previous July were repeated and magnified by increased numbers of *Sagitta neglecta* and *Tortanus barbatus*.

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* *Evadne nordmanni* was taken almost exclusively in the stomachs of specimens of *Ambassis jacksonensis* (Macleay) and *Hyperlophus vittatus* (Castelnau) collected from Black Neds Bay and Croudace Bay at the south end of the lake in August 1953, by Mr. J. M. Thomson.

Concerning the level of plankton at different stations in the lake, generally the centre of the lake (stations T.19 to C) is richest in zooplankton; and it is at these stations that species completing their cycle in the lake plankton survive longest (Fig. 4, *Podon, Evadne*). From August to October of 1953 there was a wave in the distribution of *Acartia* and *Podon* whereby the greatest numbers were found in the south at the beginning of the period, then in the middle, and finally in the north in October (Fig. 4). Subsequently they settled back to the middle region of the lake. A similar wave was apparent for *Sagitta neglecta* from January to March; and for *Acartia clausii* again from March to June 1954.

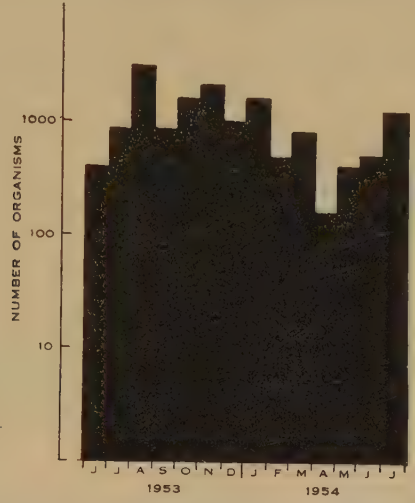

Fig. 3.—Total of average numbers of organisms from 400 l. of water for each month of the survey; plotted logarithmically.

The total zooplankton density in Lake Macquarie, however, is comparatively small, ranging from 500 organisms/400 l. (including mollusc larvae) to 4000 organisms/400 l. including decapod larvae and coelenterates, compared with a maximum of 100,000 organisms/400 l. at Port Stephens. High values in the Port Stephens zooplankton are due particularly to large numbers of *Temora turbinata, Evadne tergestina*, and *Penilia schmackeri* (Fig. 5), which do not flourish in the lake. The level of nutrient salts in Lake Macquarie is relatively high (Rochford 1955) and the phytoplankton population is also apparently high. That the zooplankton fauna cannot be directly correlated with these high values may be due to the specialized physiognomy of the environment; and although the fauna is derived from the sea, not all the components of the onshore marine fauna flourish in the lake. Therefore there is a different balance of fauna and flora in the lake from that found normally in the sea.

(v) *Vertical Distribution.*—Owing to the shallowness of Lake Macquarie, there is no very marked variation in vertical distribution of zooplankton.

In August, however, surface plankton hauls at either end of the lake were dominated by *Acartia clausii*, and in hauls from 5 m and deeper the plankton was dominated by *Gladioferens brevicornis*. During the same month at station P.22, when *Acartia clausii* was considerably reduced in the surface plankton it was especially rich in the haul from 5 m. The same phenomenon was observed with the distribution of *Acartia clausii* in November at station D and in March at stations D and M.24. In March and July 1954, *Sagitta neglecta* was found more plentifully in the deeper hauls.

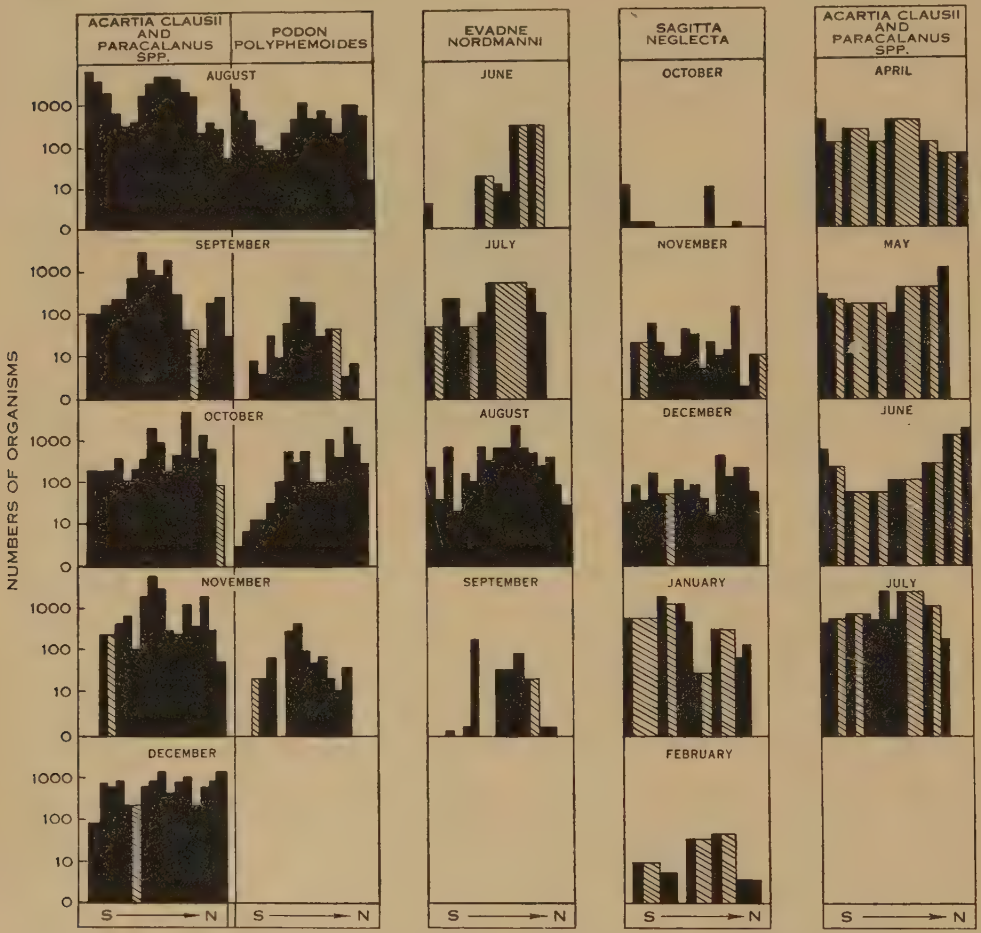

Fig. 4.—Numbers of certain species at each station, south to north throughout the year, showing succession of numerical peaks from south to north of the lake; plotted logarithmically. Hatched areas indicate stations hauls not taken.

In all cases, this distinctive vertical distribution disappeared in the following months when the hauls were taken at the same time of day at the same depths, and when species concerned were equally distributed at all depths. Therefore, it is not apparently due to diurnal migrations. It may be related to discharge of water and nutrients from Dora Creek and Cockle Creek; which may also be related to the wave form of the highest concentration of species from south to north which has been mentioned above.

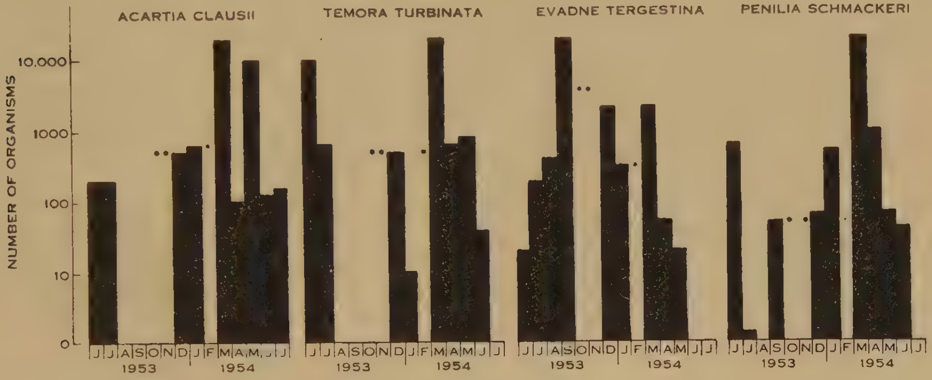

Fig. 5.—Numbers of the dominant zooplankton species from 400 l. of water at the Port Stephens station from June 1953 to July 1954 (for comparison with Fig. 1); plotted logarithmically. Asterisks indicate months hauls not taken.

VI. Conclusions

It is therefore suggested that the zooplankton of Lake Macquarie is a particularly specialized, perhaps relict fauna, derived from the sea fairly recently (absence of *Sulcanus conflictus*) and containing elements of the onshore marine zooplankton associations no longer common so far north; affected little by the current marine fauna; and little affected by the small freshwater flow into the lake.

Physical features which may be responsible for the isolation of this fauna are: (*a*) seasonal dilution of the lake with creek and rain water; (*b*) shallowness of the lake and consequently high diurnal and annual temperature ranges. Conditions are therefore less constant than those of the sea. This will affect especially the breeding and growth of certain organisms and account for the low level of the zooplankton which is present.

VII. Acknowledgments

The author is particularly indebted to Professor Baas Becking, whose suggestions have been most productive, and to Mr. D. Rochford, whose advice has always been most stimulating. Thanks are due also to Mr. W. Nelson, State Fisheries Inspector at Lake Macquarie, and to Mr. K. Champion and Mr. G. Kitchen and other members of the Division of

Fisheries, C.S.I.R.O., for indispensable assistance in the field; and to Miss B. McGrath and Mrs. Patricia Wyllie, who assisted in handling the material in the laboratory. Dr. M. Blackburn and Mr. J. M. Thomson identified the coelenterates and chaetognaths respectively.

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THE EFFECTS OF ARTIFICIAL ENRICHMENT OF A LAKE

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Summary

A Tasmanian highland lake of low natural productivity was enriched by the addition of a mixture of chemicals. The first application, to the mud, stimulated the existing stunted aquatic vegetation to produce a prolific growth; a later application, broadcast over a portion of the lake, had the additional effect of increasing phytoplankton and zooplankton.

Concurrent with the growth of plants there was a marked increase in the total numbers of epiphytic fauna.

Fish living in the lake at the time of enrichment showed a marked increase in growth rate, and others released later showed a similar response.

It is tentatively concluded that phosphorus was the element responsible for the stimulus to the growth of plants and plankton. It is shown that an unproductive lake of this type can, by suitable enrichment, be rendered capable of carrying a stock of fish.

I. INTRODUCTION

There have been several attempts to increase the productivity of natural waters including, among the more successful, the work on sea lochs by Gross *et al.* (1947, 1950) and on lakes by Juday, Schloemer, and Livingston (1938), Smith (1945, 1948), Ball (1948), and Langford (1948). Huntsman (1948) even added fertilizer to a section of a river with apparent effect. In America fish ponds have often been enriched successfully (see, for example, Swingle 1947), and empirical enrichment methods have been in use in Europe for centuries (Nees 1946).

Early in 1948 the Division of Fisheries, C.S.I.R.O., began an experiment to increase the productivity of a Tasmanian freshwater highland lake by adding fertilizers.

Lake Dobson (42° 41′ S., 146° 35′ E.), some 50 miles from Hobart, in a National Park, was selected for this study. It was known that although attempts had been made to stock this lake with trout these had met with little success, and it was thought when the investigation started that the lake was practically devoid of fish. Although low-level lagoons at first seemed more suitable because of the better scope for practical extension of the results, all those examined proved too shallow and impermanent.

This lake is 3382 ft above sea-level; it has an area of 14.5 acres, a maximum depth of about 20 ft, and a capacity of approximately 30.1 million gallons. The water is derived mainly from surface run-off, soakage, and a number of small streams coming mostly from Mount Mawson, which rises 1000 ft from the western shore of the lake. Of the streams, Eagle

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Tarn Creek in the north and Golden Stairs Creek in the west served as indicators of the properties of the waters feeding the lake. The former is mainly subterranean and flows from the tarn of that name, situated some 200 yd north of Lake Dobson. The lake is a glacial formation in dolerite, dammed at the southern end by a terminal moraine. Lewis (1921) has recorded the geology of the National Park, including Lake Dobson.

The programme of work on this lake included a preliminary study of conditions in the lake for at least 1 year, to be followed by enrichment and eventually, if this proved successful, by the introduction of fish.

II. METHODS

(*a*) *Stations*

Three stations were occupied at approximately monthly intervals throughout this study; their positions are shown in Figure 1. Station I, at the northern end of the lake, had a depth of about 4 ft; station II, near the centre, was over the deepest part of the lake; and station III, near the outlet, was in about 4 ft of water. At station II samples were taken from deep water as well as from the surface. Eagle Tarn Creek and Golden Stairs Creek were also normally sampled, at their points of entry into the lake. Samples were collected in the afternoon.

(*b*) *Physical Factors*

(i) *Temperature.*—This was measured with a reversing thermometer at each station on each occasion that a water sample was taken, and at certain other times.

(ii) *Outflow.*—The flow of water through the lake was measured 105 times from May 1950 to October 1953, from a gauge installed by the Hydro-Electric Commission of Tasmania.

(*c*) *Chemical Factors: Water Analysis*

(i) *Total and Fixed Solids.*—These were estimated by the conventional analytical procedure of evaporating at 180°C for total solids, then igniting at 500°C for fixed solids.

(ii) *Oxygen.*—This was estimated by Winkler's method. Percentage saturations were assessed with the aid of Rawson's (1944) nomogram.

(iii) *Phosphorus.*—Until May 1951 the inorganic and organic phosphorus was determined as described by Rochford (1951). Thereafter only inorganic phosphorus was determined.

(iv) *pH.*—This was measured potentiometrically until April 1951, from samples collected in wax-lined bottles, immediately on receipt in the laboratory. Thereafter pH was measured colorimetrically in the field, using bromothymol blue as indicator.

(v) *Alkalinity.*—This was determined by titrating samples with hydrochloric acid, and expressed as calcium bicarbonate alkalinity.

(*d*) *Chemical Factors: Mud Analysis*

The following were determined on oven-dry samples of mud from each station: per cent. ignition loss; per cent. organic matter (Walkley and Black method; see Piper 1947); per cent. total nitrogen (Piper 1947); per cent. ferric and aluminium hydroxides; phosphorus in p.p.m. (MacGregor 1950); per cent. calcium (as CaO); and the acid-insoluble fraction.

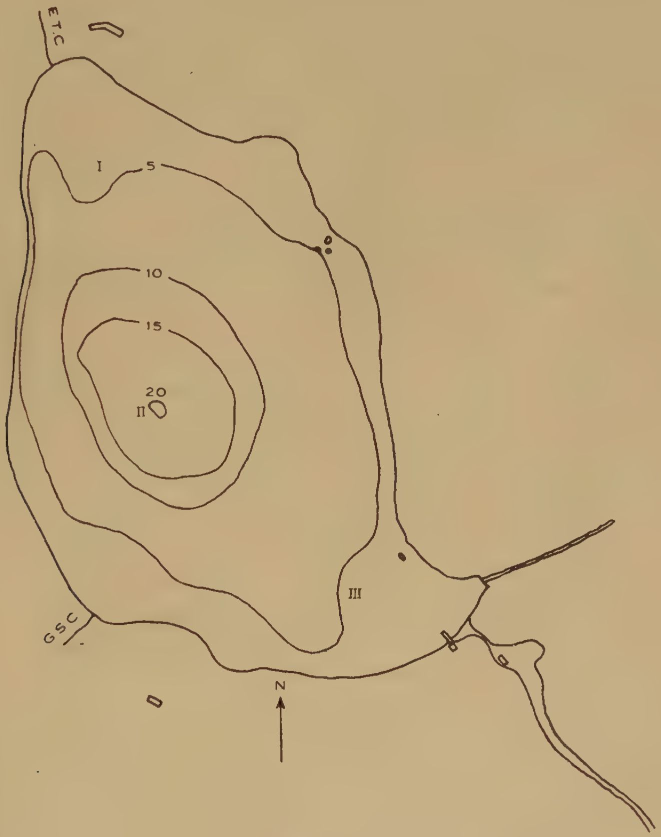

Fig. 1.—Map of Lake Dobson showing the depth contours in feet. Stations are indicated (I, II, and III), and the points of entry of Eagle Tarn Creek (E.T.C.) and Golden Stairs Creek (G.S.C.) are shown. 1 in. = 6 ch.

(*e*) *Chemical Factors: Special Studies*

(i) In order to trace the fate and distribution of the added phosphorus in relation to the plant growth stimulated by the enrichment, a special mud sampler was used to take samples at depths of 1, 2, and 3 ft, and at distances of 0, 3, and 6 ft from the centre of a typical plant clump in November 1950. The sampler was designed to collect mud at the required depth and bring it unpolluted to the surface.

(ii) In October 1952, samples of the plant *Myriophyllum elatinoides* Gaud. were collected for analysis; these were dried in the laboratory and analysed quantitatively for silicon, iron, aluminium, calcium, magnesium, sodium, potassium, chlorine, sulphur, and phosphorus. Protein (N × 6.25), ash, and water content were also determined.

(*f*) *Biological Factors*

(i) *Phytoplankton.*—Water samples for phytoplankton counts were collected from November 1950 to September 1952 from all stations, at first by Nansen reversing bottle and later with a specially constructed bottle of 6 l. capacity. Samples were immediately transferred to glass bottles and sufficient formalin added to make a 5 per cent. solution. Until March 1952, duplicate samples were centrifuged for counting. After this the sedimentation method with inverted microscope was used, for which 5-ml samples were sufficient. This was much more economical of time and effort, and tests indicated no important discrepancy between results obtained by both methods on similar samples. Results are expressed in logarithms of diatom numbers per litre.

(ii) *Zooplankton.*—Nine-minute oblique plankton tows (three 3-min tows of equal distance through deep, mid, and surface water) around a course marked by two buoys at station II were begun in April 1948 and repeated, generally at monthly intervals, until September 1952. A conical silk net of 40 meshes/linear inch and with an opening of 30 cm diameter was used. The plankton hauls were preserved in 5 per cent. formalin and later sorted, identified, and counted in the laboratory. Results are expressed as numbers per tow, the speed and distance of tows always being approximately the same.

(iii) *Bottom Fauna.*—From September 1951 until September 1952, 22 samples were collected from the usual stations and from certain other regions in the littoral. A hand-operated grab which covered 1 sq. ft when open was used to collect the samples. A Petersen type grab was used in the deep water at station II. All samples were preserved with formalin in the field. In the laboratory as much as possible of the mud and debris of the sample was washed away through a wire sieve (40 meshes/linear inch) and the remainder searched for animals. These were sorted, counted, and weighed wet (after excess moisture had been removed) and preserved in 5 per cent. formalin. Results are expressed in numbers and weights per sq. m.

(iv) *Plant Fauna.*—Nineteen plant samples (*Myriophyllum*) were collected from September 1951 to September 1952, from several places in the shallower parts of the lake. These were taken with a grab similar to that described by Macan (1949), but modified by the addition of gauze-covered windows on the sides to allow the water to drain off without loss of fauna. The sample was preserved in formalin immediately after collection.

In the laboratory the samples were stripped of their fauna, excess moisture was removed, and the plant sample was then weighed. The epifauna was counted and weighed, and preserved in 5 per cent. formalin. Results are expressed in numbers and weights of animals per kg of wet plant (excess moisture removed).

(v) *Fish.*—In May 1952, 467 yearling brown trout were released in the lake. These had been reared at the Plenty Hatchery of the Salmon and Freshwater Fisheries Commission from ova stripped at the Great Lake in May 1951. Before being released each was tagged by a modification of Shetter's (1936) jaw-tag method, in which the tags were not rounded after application but left flat, as experience has shown that they are carried better this way by fish from 4½ to 6½ in.

III. Conditions Prior to Enrichment

Figure 2 gives the temperature conditions in the lake for the period of the investigation. Considerable seasonal fluctuations are revealed, but as shown in Figure 10 there was no stratification, the temperature of the bottom differing only a little from that at the surface throughout the year.

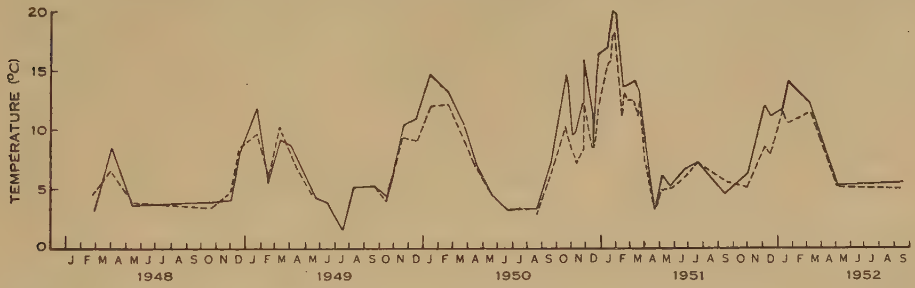

Fig. 2.—Temperature conditions in Lake Dobson. —— Surface; — — bottom. Each surface value is the mean for all stations.

Over the period of 30 months during which the lake was studied, the mean outflow of water was 741,733 gal/day.

Values for inorganic and organic phosphorus in the lake water, compiled from data given by Rochford (1952*a*, 1953*a*), are given in Figure 3, which shows that prior to enrichment neither reached 10 μg/l. The graph indicates that there is considerable correspondence between higher values for organic phosphorus and lower values for inorganic phosphorus, and vice versa, suggesting organic utilization of phosphorus in the water followed by degeneration and return to the water of phosphorus, first in organic and subsequently in inorganic form.

The mud of this lake is deep, flocculent, and very soft. Its chemical composition, given in Table 1, reveals the presence of phosphorus and other nutrients, which were apparently unavailable for plant growth in its natural state. A considerable proportion of the mud has been formed from organic material (leaves and other vegetable matter) washed in, as can be seen on examining the bottom samples. Microscopic examination of the mud reveals the presence of huge numbers of diatom shells of species now apparently extinct in these waters.

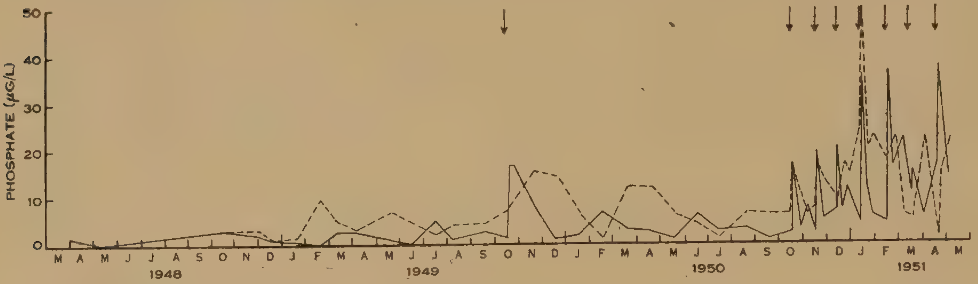

Fig. 3.—Inorganic and organic phosphorus levels in the water of Lake Dobson. ——— Inorganic; — — organic. The arrows indicate the dates of enrichments referred to in the text. Each value is the mean for all stations.

Values in Table 1 are from post-enrichment samples. It will be shown later that the quantities of fertilizer used and the methods of application were such as to have little if any effect on the gross composition of the mud.

TABLE 1

CHEMICAL ANALYSIS OF LAKE DOBSON MUD
Oven-dry*

Station	Ignition Loss (%)	Organic Matter (%)	Total N† (%)	C:N Ratio	Fe and Al Oxides (%)	P† (p.p.m.)	CaO (%)	Acid-insoluble (%)
I	23.1	15.2	0.57	15.5	5.75	270	0.78	67.3
II	23.9	19.2	0.67	16.6		260		
III	8.7	5.5	0.17	18.9		160		

* All further references to percentage composition of muds in this paper will signify per cent. of dry weight.

† Means of a number of samples for each station.

Prior to enrichment the higher plants of the lake consisted of a comparatively small number of stunted specimens of *Myriophyllum elatinoides* restricted mainly to the northern end. Some small scattered *Isoetes* grew in the littoral.

Little factual information is available as to the quantity of organisms available for fish food in the natural lake. Plankton was known to be low, as will be shown later, and the limited quantity of aquatic plants could have provided only a very small amount of epiphytic fauna for fish.

The history of attempted stocking of this lake, obtained from the records of the Salmon and Freshwater Fisheries Commission, shows that in 1930 "70,000 Brown Trout Fry were released in the Lakes". There are numerous lakes in this Park, and it may be assumed that Lake Dobson received a portion of this consignment. In 1940, 100,000 rainbow trout fry were released in Lakes Fenton and Dobson. The former is by far the larger lake (about 10 times the area of Lake Dobson) and may be assumed to have had the bulk of this batch of fry.

At the time when the experimental work started it was known that these fish had not found conditions very suitable, and that they had not reproduced to any great extent. On occasions when the lake was visited between 1947 and 1950, trout were seen in numbers varying from a few to a dozen.

If these fish were the progeny of the early liberations they must have been spawned in the outlet of the lake, where the Broad River begins, as this is the only place where gravel is available. It is conceivably possible that these fish were upstream migrants from the Derwent River, into which the Broad River flows, but conditions in the Broad River only a few hundred yards from the lake are such as to make the success of any such upstream migration exceedingly doubtful. At this point the river tumbles down an irregular slope which is part of the terminal glacial moraine, and thus provides no pools to aid fish in the ascent. At no time is the flow of water from the lake of sufficient volume to assist fish in overcoming this obstacle.

To ensure that no trout entered the lake, the river was screened at this point with wire netting of $\frac{1}{2}$ in. mesh; the screen was placed in position in 1947 and renewed in 1952.

Native trout (*Galaxias* sp.) are abundant in Eagle Tarn above Lake Dobson but were never seen in the lake in comparable quantities. It is possible that they had been more numerous originally, and that the introduced trout had greatly reduced the stock.

IV. CHEMICAL ENRICHMENT

On October 19, 1949, 1740 lb of a fertilizer with the following composition was placed in the lake in paper bags, each containing approximately 10 lb of the mixture:

40 parts of ammonium sulphate,
60 parts of superphosphate (20.5 per cent. water-soluble P_2O_5),
5 parts of potassium chloride,
15 parts of ground limestone.

This is the mixture given by Davison (1943) except that the superphosphate in his mixture contained 16 per cent. water-soluble P_2O_5.

The bags containing this mixture were dropped from a rowing boat which described two traverses of the lake parallel to the approximate north-south axis, and two traverses at right angles to this axis.

It was hoped that the bags of fertilizer would penetrate the soft mud of the lake and be used only slowly and sparingly, and that some of the nutrients naturally present in the mud might be converted to more biologically available forms and released.

The second enrichment was made as a series of monthly additions from October 1950 to April 1951. The same total amount of the same mixture as in 1949 was used, and was broadcast evenly over the northern part of the lake.

Crushed limestone was added to the northern part of the lake three times between October 1951 and January 1952, the total amount used being 1 ton (2240 lb).

V. Effects of Chemical Enrichment

(*a*) *Water*

(i) *Oxygen.*—Analyses made on samples collected from April 1950 to September 1952 indicate clearly a rise in percentage saturation of oxygen in the water. This is shown in Figure 4.

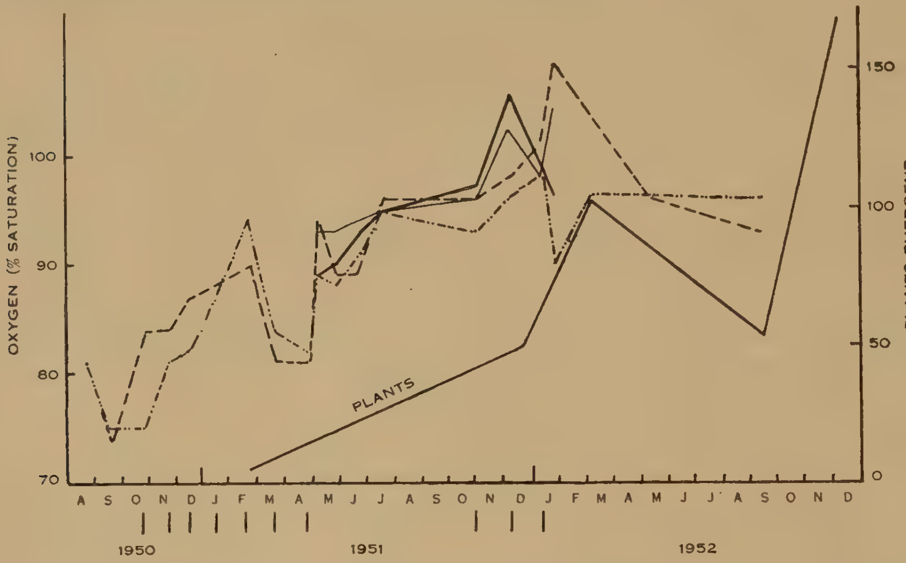

Fig. 4.—Oxygen per cent. saturation in Lake Dobson. —— Station I; station II, — — surface; —. .— bottom; ——— station III. The number of plants reaching the surface is also figured. Small vertical lines indicate enrichment dates.

Oxygen samples were collected early in the afternoon. It cannot be claimed that any one value is significant in itself. However, it is believed that the general picture over many months quite reliably indicates a gradual increase.

(ii) *Phosphorus.*—Figure 3, compiled from data given by Rochford (1952*a*, 1953*a*), indicates that prior to the addition of fertilizer in bags in 1949 the total phosphorus values did not exceed 10 μg/l. In October 1949 a sharp pulse in inorganic phosphorus followed the addition of fertilizer in bags, and this was accompanied by an increase in organic phosphorus level of much longer duration. After the effects of the 1949 enrichment had declined, the dynamic inorganic-organic phosphorus relationship hypothesized in Section III apparently operated again until October 1950. From then until April 1951 the record shows clear correspondence in both inorganic and organic phosphorus levels with monthly additions of fertilizer, characterized by swift elevations of both phosphorus fractions and with early and steep drops in both. From April 1951 until September 1952 only the inorganic phosphorus level was determined; this was consistently less than 10 μg/l.

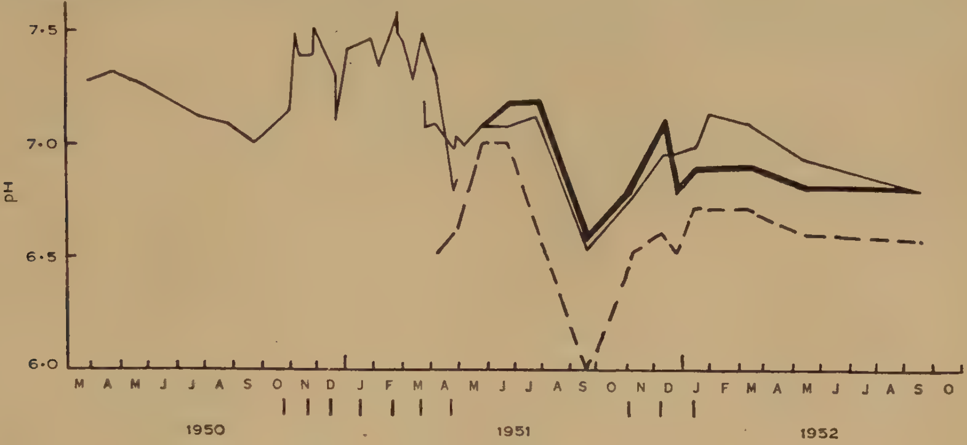

Fig. 5.—pH during the course of the experiment. ——— Mean of values for all stations in Lake Dobson; —— Golden Stairs Creek; — — Eagle Tarn Creek. Small vertical lines indicate enrichment dates.

(iii) *pH.*—Figure 5 shows that the pH of the lake rose slightly following the enrichment of 1950-1951, though it fell again in March and April 1951 even before the series of additions was completed, suggesting that the change was merely seasonal rather than fertilizer-induced. Data from the three stations on several occasions immediately before and after fertilizer additions (1950-1951) showed no change that could be obviously related to these. These data are not included in Figure 5 as they would merely complicate the picture unnecessarily. Where the enrichments coincided with the pH sampling, the pH given in Figure 5 is that taken *before* enrichment. The pH of the lake stayed close to that of Golden Stairs Creek, and its changes were generally paralleled by changes in the inflows. From December 1951 to May 1952 the pH of the lake exceeded that of Golden Stairs Creek. This rise followed the 1951-1952 liming of the lake.

(iv) *Alkalinity.*—Alkalinity (as $Ca(HCO_3)_2$) varied little from July 1951 to September 1952, standing at an average of 19.5 mg/l., although the level was always somewhat higher than those of Eagle Tarn and Golden Stairs Creeks (means standing at 16.8 and 12.8 mg/l. respectively). No determinable response followed the addition of ground limestone.

(*b*) *Mud*

Results of mud analyses from April 1948 to March 1951 are given by Rochford (1952*b*, 1953*b*). Unfortunately the methods were those used in his studies of estuarine muds and proved unsuitable for the lake muds. Moreover, insufficient samples were taken to gain a reliable and comprehensive picture of pre- and post-enrichment composition. In later samples analyses were done on the whole mud and the results are given in Table 1. It suffices to state that none of the methods of collection or analysis served to show any generalized or widespread changes in the chemical composition following additions of chemicals to the lake.

(*c*) *Special Chemical Studies*

(i) The mud samples taken around the plant clump on November 20, 1950, to determine the fate of the phosphorus, revealed the data given in Table 2 supplied by Mr. D. Rochford.

TABLE 2

DISTRIBUTION OF ELEMENTS AROUND THE BASE OF A MYRIOPHYLLUM CLUMP

Distance from Centre of Clump (ft)	Depth (ft)	Phosphate Phosphorus			Total Ferric Iron (mg/g silt)	Organic Carbon (mg/g silt)	Total Nitrogen (mg/g silt)	Silt (%)
		Interstitial (μg/g mud)	Adsorbed (μg/g silt)	Total (μg/g silt)				
0	1	271	290	1000	6.0	55	6.4	64
	2	16	90	228	7.1	57	5.6	75
	3	1	49	168	5.6	65	6.6	69
3	1	7	31	181	9.0	54	5.3	61
	2	5	3	238	6.3	63	5.2	75
	3	12	29	224	9.6	60	5.2	94
6	1	16	16	96	10.8	47	4.3	50
	2	3	70	196	8.4	63	6.9	80
	3	7	21	126	9.0	46	5.0	78

Most of the phosphorus (interstitial, adsorbed, and total, determined by Rochford (1951)) was apparently concentrated 1 ft below the surface at the centre of the clump.

(ii) The analysis of the *Myriophyllum* plants collected as described in Section II(*f*) (iv) gave the data given in Table 3.

(*d*) *Biological Effects*

(i) *Phytoplankton.*—Phytoplankton declined from a very high value immediately following the 1950-1951 enrichment (Fig. 6). Although lack of pre-enrichment records obscures the issue it appears likely that the graphed data represent an initial large pulse following enrichment, with subsequent decline to a lower level. Diatoms made up the bulk of the phytoplankton, and although desmids, filamentous green algae, *Tetraspora*, blue-greens, and zooflagellates were noted sporadically the frequency of their occurrences was insignificant.

On June 2, 1954, samples were taken from all stations and seemed to show that there had been no decline since 1952.

TABLE 3

COMPOSITION OF MYRIOPHYLLUM SAMPLES FROM LAKE DOBSON

Results expressed as percentages of oven-dry plant

Component	Sampling Position		
	Unenriched	Doubtful	Enriched
Protein (N × 6.25)	17.9	13.9	21.8
Ash	13.5	14.8	13.7
Silicon*	0.49	0.66	0.07
Iron	0.10	0.08	0.04
Aluminium	0.13	0.14	<0.01
Calcium	3.22	3.21	2.61
Magnesium	0.36	0.47	0.39
Sodium	0.33	0.36	0.60
Potassium	0.29	0.41	0.33
Chlorine	0.54	0.62	0.69
Sulphur	0.19	0.12	0.19
Phosphorus	0.04	0.05	0.14
Water†	92.0	91.3	92.5

* The silicon values may owe their variations partly to contamination effects.

† Approximate percentage in fresh material.

(ii) *Zooplankton.*—From April 1948 to September 1950 the zooplankton level was very low (Fig. 7). From then on some notable increases have occurred. Prior to October 1949 the average plankton catch was 25 organisms, mainly copepods. No change followed the enrichment of that month (in bags), the average up to October 1950 being 24. During and immediately after the second enrichment (broadcast) the average number per tow was 141. From November 1951 to September 1952 the average was 900. On March 23, 1954, a tow revealed the second highest catch recorded, 2377. The zooplankton always consisted almost entirely of copepods.

(iii) *Bottom Fauna.*—Bottom fauna records extend from September 1951 to September 1952, so that nothing is known of the pre-enrichment level. Twenty-two samples were collected. The bulk of the weight of fauna was easily dominated by the Pulmonata, followed by the Eulamellibranchia, Chironomidae, and Amphipoda, though in numbers the latter three groups each considerably exceeded the Pulmonata. The mean number of animals per sq. m was 571; the mean weight per sq. m was 3.9 g, that is, 35 lb/ac or 39 kg/hectare. Samples taken in June 1954 showed that the bottom fauna was relatively unchanged.

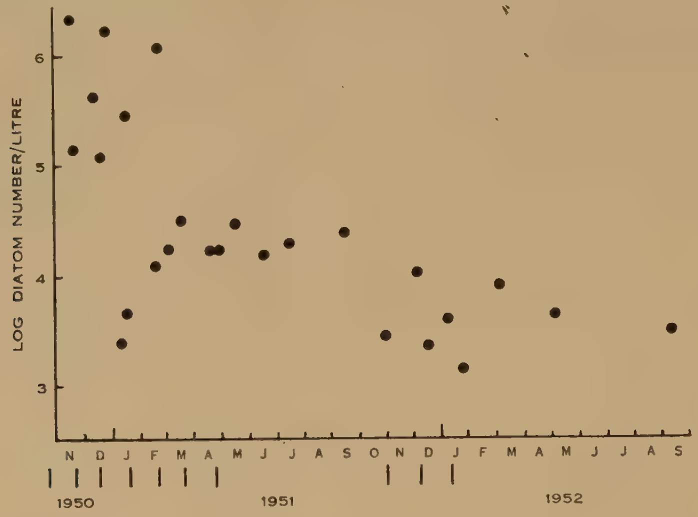

Fig. 6.—Phytoplankton in Lake Dobson following enrichment. Each of the points represents the mean for all stations on a particular date. Small vertical lines indicate enrichment dates.

(iv) *Higher Aquatic Plants and Associated Fauna*.—In the year following the first addition of fertilizer (October 1949) a very distinct pattern of clumps of the flowering aquatic plant *Myriophyllum elatinoides* appeared. The clumps grew in the lines of the traverses which were described in 1949 when the bags of fertilizer were dropped in the lake.

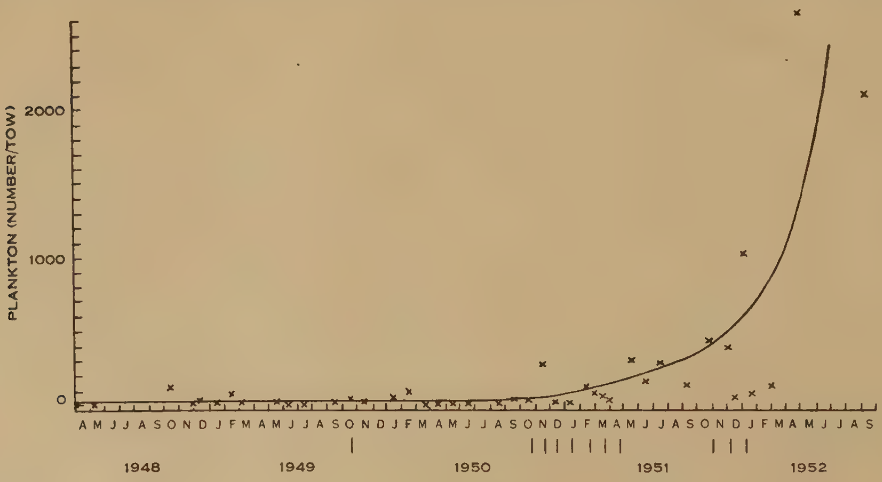

Fig. 7.—Zooplankton in Lake Dobson. The short vertical lines indicate enrichment dates.

In April 1952 the clumps were about 5 ft across and weighed approximately 60 lb when wet. Many of the clumps have since grown considerably and some have reached the surface through as much as 12 ft of water.

Since the 1950-1951 enrichments the northern part of the lake has developed a profuse growth of *Myriophyllum* plants in addition to those in the traverse lines of 1949. Many of these newer plants, though they started their rapid growth about a year later, are now (1954) comparable with the April 1952 size of the plants in the lines.

The number of plants breaking the surface of the lake was used as a rough growth index, as seen in Figure 4. Numbers rose from early 1951 to about 160 in December 1952. At present (1954) the coalescence of many of the clumps, especially in the north part of the lake, and the great number emergent make reliable counting difficult. The estimated numbers of emergent clumps is at least 250. Plate 1 shows the position in December 1952.

The animals associated with the plants were sampled from three positions near the northern end of the lake, and from other littoral regions. The sampling plan was not systematic and was changed somewhat during the period of the collections, but from September 1951 to September 1952, 19 samples were collected.

Pulmonata easily comprised the bulk of the plant fauna by weight and number, with Plecoptera ranking next. Amphipoda and Trichoptera followed but were much less important. Other groups were found less frequently, such as Porifera, Hydrida, Copepoda, Coleoptera, Neuroptera, Ephemeroptera, Diptera (chironomid larvae and pupae), Hydracarina, Eulamellibranchia, and Anura.

The mean number of animals per kg of wet plant was 1488 and the mean weight per kg was 5.3 g.

Samples taken in June 1954 showed that the plant epifauna was generally unchanged.

VI. The Growth of Fish

The 467 tagged yearling brown trout were released in May 1952, about 14 months after the plants first reached the surface in the shallower parts of the lake.

At tagging, the mean length of the fish was 12.6 cm (5.0 in.), and their mean weight was 20.2 g (0.7 oz). Their length range was from 10.4 to 18.6 cm (4.1-7.3 in.) and the range in weight was from 10.8 to 75.6 g (0.4-2.7 oz).

In January 1954, after they had been in the lake for 1 year and 8 months, a sample was obtained from the lake by means of a net. A linen gill-net (graball) was used, some 35 yd long, of 2¼ in. mesh, with 100 meshes drop (about 10 ft when set). Between January 18 and 30 this net was set on 11 occasions during the late afternoon and lifted the following morning, and 35 fish were captured. All fish were measured, weighed, and sexed, and scales were taken for age determination and growth measurement.

The total catch comprised: 18 brown trout bearing tags, 5 brown trout which had lost their tags, 11 brown trout which had not been tagged, and 1 rainbow trout which had not been tagged.

Since, at that time, the tagged fish were not 3 years of age, and it was desirable to have information on their growth during three complete years, a further attempt to catch fish was made during May 1954. The net was set on May 15 and lifted daily for examination, and between May 16 and 19, 14 fish were taken. The water temperature then fell to a little above freezing owing to a heavy fall of snow, and no more fish were taken as they cease to move during such cold periods.

TABLE 4

AGE OF FISH TAKEN FROM LAKE DOBSON

Year Class: Age (yr):	1945 9	1946 8	1947 7	1948 6	1949 5	1950 4	1951 3	1952 2	Total
Males	2	—	1	3	4	—	14	3	27
Females	1	1	—	1	2	1	14	—	20
Not sexed	—	—	—	—	—	—	2	1	3
Total	3	1	1	4	6	1	30	4	50

The 14 fish comprised: 4 brown trout bearing tags, 3 brown trout which had lost their tags, and 7 brown trout which had not been tagged.

The full data for these 49 fish, including their scale readings, are given in Appendix I, which also includes data on two fish which were found spawning in 1952 and removed from the lake when the tagged fish were released. From their scale readings the fish were classified into age groups, and this information is summarized for the 50 brown trout in Table 4, in which their age is expressed both as regards the year of spawning and the age which they had, or would have, attained by May 1954.

When possible the younger tagged fish were returned to the lake, which explains why some were not sexed.

It will be seen that (excluding the single rainbow) 40 per cent. of the catch was composed of fish which had not been tagged. These fish must all have been in the lake at the time the tagged fish were released. The rainbow was almost certainly accidentally included among the tagged fish; the latter were held in the hatchery troughs from May 7 until their release on May 19, and during that time it is not improbable that the rainbow jumped over from an adjacent trough. The possibility of its being a descendant from earlier stocking cannot be excluded, but no other rainbow trout have been taken from the lake.

The probability of fish having entered the lake from the Broad River has been excluded, from which it follows that those fish of more than 3 years of age in May 1954 and the four younger fish which had not been tagged are descendants of the original stocking.

TABLE 5

MEAN LENGTH AT EACH YEAR OF TROUT FROM LAKE DOBSON

Year Class	No. of Fish	Mean Lengths* (cm) L_1	L_2	L_3	L_4	L_5	L_6	L_7	L_8	L_9	$L_{Jan.}$
1945	3	10.7	20.5	27.2	36.0	*44.7*†	50.3	55.0	60.0‡	65.0‡	—
1946	1	10.5	25.0	40.5	*48.5*	52.5	57.0				—
1947	1	16.5	24.5	*28.5*	36.5	48.0	52.5				54.5
1948	4	10.6	*19.9*	36.6	47.8	53.6	58.0‡				—
1949	6	*12.5*	28.3	42.3	50.1	54.5‡					—
1950	1	11.5	26.5	36.5							40.5
1951	23	14.1	28.1								33.8
	7	13.2	27.1	35.0							—
1952	4	19.0‡	30.9								—

* L_1-L_9, mean lengths for each year of fish 1-9 years of age; $L_{Jan.}$, length at capture of fish taken in January 1954, which had not completed a full year's growth.

† Italicized figures are values for mean lengths attained by fish of each age group in 1950, during which year enrichment was taking place.

‡ Value based on fewer than total number of fish in group.

Table 5 shows the mean lengths for each year of all the fish of each age group shown in Table 4, derived from a study of their scales.

TABLE 6

COMPARISON OF GROWTH BEFORE AND AFTER ENRICHMENT

Group	Mean Length at Each Year: Before Enrichment: No. of Fish	Before Enrichment: Mean L (cm)	After Enrichment: No. of Fish	After Enrichment: Mean L (cm)
L_1	9	11.3	4	17.1
L_2	5	22.2	11	29.1
L_3	4	30.5	11	39.7
L_4	3	36.0	11	48.0

The data given in Table 5 are plotted in Figure 8, on which has also been indicated the beginning and ending of the addition of fertilizer to the lake, the approximate time of the first observed effect of such addition on the growth of plants, and the date at which the first of the plant clumps reached the surface.

It will be noted, particularly in the younger age groups of fish, that a distinct upward trend in the growth rate follows on the stimulation of plant growth. This can best be illustrated by comparing the mean lengths of fish for each year before the increase in plant growth with the mean lengths of the corresponding ages after enrichment, given in Table 6.

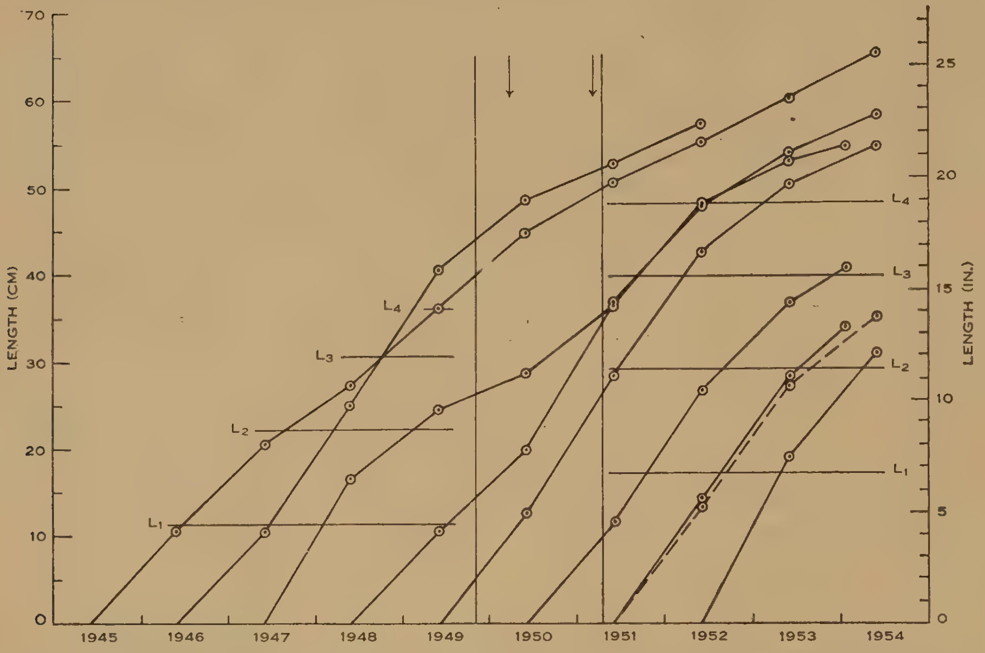

Fig. 8.—Calculated mean lengths at each year of all brown trout taken from Lake Dobson. Horizontal lines indicate the mean lengths of all fish of the same age before and after enrichment. Vertical lines indicate the beginning and ending of the addition of fertilizers, and the arrows the approximate dates of first observed effect on plant growth and first plants to reach the surface. The broken line represents the means for the seven fish of the 1951 year class which had completed 3 years' growth at capture.

It should be noted that in arriving at these figures, all values for fish which completed a year's growth during the actual period of enrichment (those in italics in Table 5) have been excluded, since this transition period must have had some effect on growth and yet its full effect could not have been exerted. These figures could not, therefore, be fairly used either as pre- or as post-enrichment values. Also excluded from this comparison are the figures for the tagged fish released in the lake; these were reared in the hatchery for their first year, and therefore did not represent growth under lake conditions, and this handicap would have some influence on subsequent years.

These mean values are indicated in Figure 8 by means of horizontal lines drawn through the appropriate values, labelled L_1, L_2, etc., and are also plotted in Figure 9, where they are compared with data from other sources.

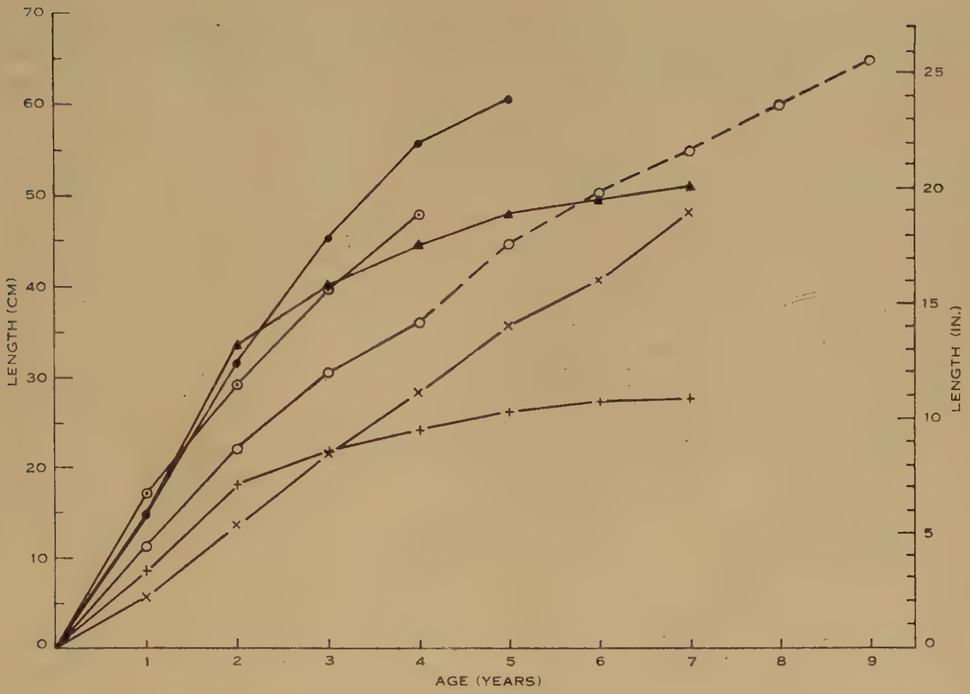

Fig. 9.—Comparison of growth rate of trout in Lake Dobson, before and after enrichment, with trout from Brady's Lake, Lake Leake, Lake Windermere, and Three Dubs Tarn. The post-enrichment growth of those fish which had attained 4 years of age prior to enrichment is shown as a broken line. Lake Dobson, ○ before enrichment, ⊙ after enrichment; ● Brady's Lake; ▲ Lake Leake; × Lake Windermere; + Three Dubs Tarn.

VII. Discussion

The total and fixed solids in Lake Dobson are 31 and 21 mg/l. respectively. This is rather close to the lower limits for concentrations of dissolved solids found in natural waters (Rawson 1951; Welch 1952). Rawson showed that total solids is a good rough guide to lake productivity. It is likely that Lake Dobson was basically unproductive because it is low in total solids. The insoluble resistant nature of the land surrounding the lake and its small catchment area account for the low total solids.

It appears that nutrients added in 1949, and more especially in 1950-1951 (broadcast), and probably most importantly the phosphate in the form of superphosphate (cf. Fig. 3), increased the phytoplankton and through it the zooplankton (cf. Figs. 6 and 7). The phytoplankton level of late 1950 and early 1951 was far higher than any subsequently. The level fell even before all the 1950-1951 additions had been completed.

This is perhaps not surprising when it is noted that the zooplankton had already begun to rise before the additions were complete.

Nees (1946) has mentioned the ion-releasing effects of lime in ponds; Macan and Worthington (1951) refer to the role of calcium in accelerating organic decomposition in muds. Hall (1947) and Russell (1950) describe how lime helps decomposition by bacteria in acid soils. Leeper (1952) showed how lime could make phosphorus more available in soil, because lime breaks down the adsorption compounds phosphorus forms with ferric iron, which are of low availability to plants. Additions of lime as described above were made because the pH of the mud from stations I and II was 6, and ferric iron was present in the surface layer of the mud.

The lime additions may have increased the plankton, for it is obvious (Fig. 7) that the zooplankton level was much higher after liming than earlier, and this was a year after the addition of the mixed fertilizer, when its effects might have been expected to have waned. Secondly, although phytoplankton fell rapidly after the 1950-1951 additions the values levelled out from October 1951. When it is realized that October 1951 also marks the beginning of the second elevation of zooplankton it must appear that while its standing crop has remained fairly constant, the *reproduction rate* of the phytoplankton must have increased from October, because the zooplankton requirements increased.

It is quite possible that the second main reason for the low natural plankton production in the lake was a poor mud-water nutrient exchange. Although the water was poor in nutrients, it could have been periodically enriched if the phosphorus and other nutrients present in the bottom deposits were released at times into the overlying water. Mortimer (1941-42) demonstrated how events occur in a stratified lake which release nutrients from mud and enrich the water during those periods of the year when the surface layer of the mud becomes reduced. He also suggested how these events may govern organic production in many lakes.

Now Figure 10 shows that Lake Dobson is unstratified. Its shallowness and the prevalence of wind action ensure this. Thus there is little opportunity for nutrients to return to the water once they have entered the mud.

Temperature records (Fig. 2) show that the water was successively warmer in the summers of 1947-48 to 1950-51. The fact that the 1950-51 summer was warm may have aided the initial utilization of nutrients added at that time but the continued increase of zooplankton through the subsequent winter and summer—and the summer of 1951-52 was cooler than that of 1950-51—suggests that higher nutrient levels (in particular phosphorus) following enrichment were the main cause of plankton response.

The plants (*Myriophyllum*) which have grown in the lake carry an important fauna and have thereby considerably improved quantitative faunistic conditions. The fauna is quantitatively and qualitatively different from the fauna of the open bottom and exists therefore only by virtue of the plants' presence.

It is not possible to say whether the present bottom fauna is better than the pre-enrichment one, as no data exist for comparison. It must suffice to say that the data for 1951-52 may be considered slightly oligotrophic (Deevey 1941; Macan and Worthington 1951).

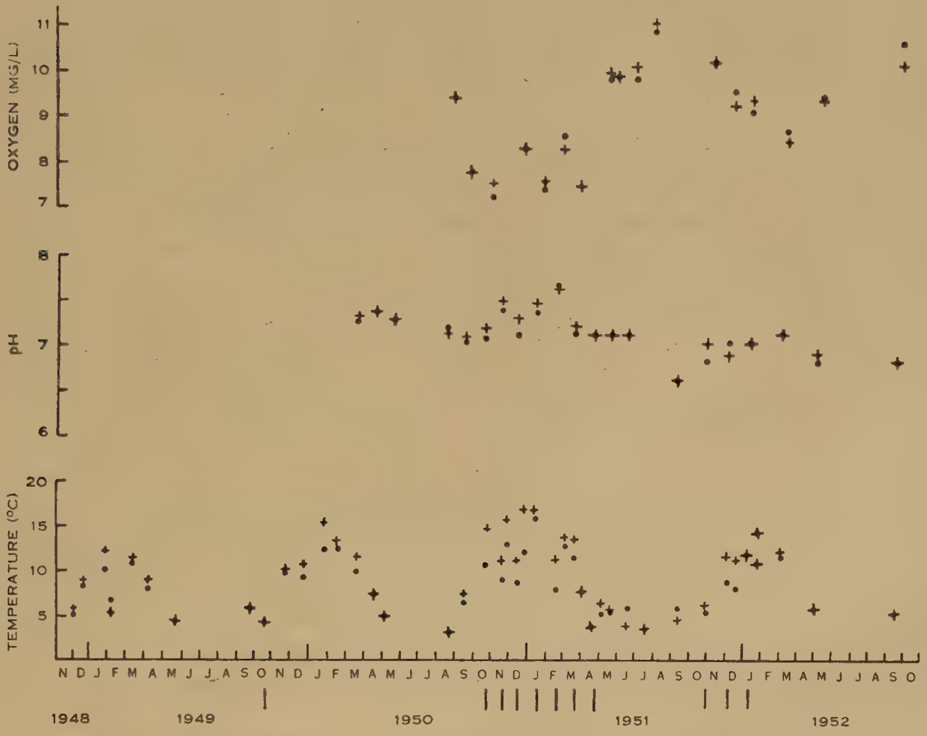

Fig. 10.—Surface and bottom water oxygen content, pH, and temperature for a range of dates, showing how slight is the tendency for stratification in Lake Dobson. + Surface; ● bottom.

A rough calculation shows how this bottom fauna could be augmented by an increase in the spread of plants. Thus the open bottom of the lake carried about 3.9 g/sq. m of animals. The plant grab, when open, covers an area of 1 sq. ft and takes samples down to approximately a foot below the top of a plant. If the average weight of animals per sample be transformed to weight per sq. m we get the value of 11.3 g/sq. m. So if the lake bottom were covered with plants to a height of approximately 1 ft, the bottom fauna would then be approximately three times greater than the natural one.

Welch (1952) refers to chemical analyses of plants as a help in understanding how much of and which elements are used by freshwater plants, and Misra (1938) employed the method in his studies of plants in the English Lakes. The method is also used in agricultural science. Accordingly, to obtain some knowledge of the mode of action of the fertilizer in stimulating plant growth, analyses of *Myriophyllum* were made (Table 3).

In this table, silicon, iron, and aluminium tend to be *lower* in plants which have come from enriched regions. If anything, this suggests that the supply of these elements did not limit plant growth. Magnesium, potassium, chlorine, calcium, and sulphur bear no particular relationship to plant development, nor apparently do protein and ash contents. However, sodium shows a slight tendency to be highest in the samples from clumps in heavily fertilized regions.

Phosphorus, of acknowledged importance in plant nutrition, is the element which bears the most striking relationship to where the plants came from and their mode of growth. It would seem, then, that lack of available phosphorus was an important limiting factor to the growth and spread of the plants before enrichment.

The mud samples collected from the base of a large clump in the traverse line (Section V(*c*)(i) and Table 2) indicated that the fertilizer (at least as regards the phosphorus) was mainly located 1 ft below the surface at the centre of the clump, and that it had not spread much in 1 year.

It was suspected at one stage that nitrogen deficiency might have been one of the limiting factors to plant development in the mud of the lake. This now appears unlikely. The nitrogen of the mud of Lake Dobson is seen (Table 1) to be 0.47 per cent. (mean). The muds of a lagoon near Hobart, and of a 40-year-old artificial lake at Triabunna on the east coast, have nitrogen values of 0.45 and 0.29 per cent. respectively. Both of these have profuse growths of aquatic plants, the latter a vast stand of *M. elatinoides*.

An interesting point is that the plants in the lake seem to have increased the percentage saturation of oxygen in the water (see Fig. 4). It is obvious that oxygen has increased with plant development. It is also of interest that the copepod fauna associated with the plant clumps seems to be specialized. While the zooplankton of the open water of station II has been mainly calanoid, a few tows among the plants in the vicinity of station I revealed a flourishing population of cyclopoids.

It will be seen that the chief effect of adding fertilizer to Lake Dobson has been to induce a flourishing growth of aquatic plants where little existed before, and that these plants carry an abundant fauna of epiphytic organisms suitable as food for certain fish. Prior to enrichment the occurrence of such plants was only sparse, and the plants themselves were stunted. The food available to fish was thus very limited in nature and extent, and at the same time little cover was provided as shelter for young fish. It is not surprising, therefore, that the original stocking of this lake with trout was unsuccessful.

It is not possible to estimate accurately the total of fish in the lake prior to the release of tagged fish. The netted samples showed 40 per cent. of the fish to have been there before, but this cannot be regarded as a true proportion because these were mostly fish large enough to have preyed upon the tagged yearlings when they were introduced, thus bringing about an unduly high mortality rate for the young fish. Throughout the discussion which follows it should be borne in mind that prior to the release of the tagged yearlings the population of the lake was small, and probably represented a natural balance between the fish and their available food. The numbers of any young which might have been added to the lake each year as a result of some limited spawning would have been quickly reduced by predation from older fish. Thus the population would tend to remain small, and at the same time the growth of fish in the lake would tend to be optimal under existing conditions.

Although Figure 8 shows an upward trend in the growth of fish after enrichment, this is not perhaps as marked as might have been expected, because with the addition of the released fish there was a substantial increase in the population.

Comparison of the mean lengths of fish at each year of age for the pre- and post-enrichment periods (Fig. 9) shows that whereas prior to enrichment the fish showed normal growth, good in the early years and declining as the fish aged, in the post-enrichment period the early growth was at a much higher rate and the annual decline was not as great. The difference was such that 3-year-old fish of the post-enrichment period were larger than 4-year-old fish prior to enrichment.

The mean growth of small samples of fish from Brady's Lake and Lake Leake is shown in Figure 9 for comparison with Lake Dobson.

It will be seen that the post-enrichment growth of those fish which had attained 4 years of age in the lake before enrichment shows a considerable increase on the pre-enrichment rate. The fish, which previously were growing at a rate considerably below that of fish in Lake Leake, have now improved to somewhat better than fish from that source though they have not attained a growth equal to that of fish of the post-enrichment period, nor to the much higher level of growth in Brady's Lake.

The difference in growth rate of fish from these three lakes is further illustrated in Plate 2, which shows photographs of scales from fish taken from these lakes. Plate 2, Figure 1, shows the steady good growth in Brady's Lake; Figure 2, the good growth in early years, falling off as the fish aged, in Lake Leake; and Figure 3, the poorer early growth in Lake Dobson, with the renewed stimulus following enrichment.

Data from Lake Windermere (Allen 1938) and Three Dubs Tarn (Frost and Smyly 1952), both from the English Lake District, are also included in Figure 9.

Frost and Smyly followed the growth rate of brown trout in a moorland fish pond enriched with bone meal. They were successful in handling much greater numbers of fish than was possible in the present case, partly because their method of enrichment did not stimulate such extensive growth of plants, so that they were able to use a seine to recover the fish.

These authors found that although there were cases of significantly increased growth rate following the additions of bone meal, the improvement was not sustained. The general picture of growth in Three Dubs Tarn is that growth was fastest during the first two years of life, and declined steadily thereafter, whereas in Lake Windermere a steady and constant growth rate was found by Allen.

It is of interest to note that growth in Lake Dobson prior to enrichment tended to show the same decline as that in Three Dubs Tarn, although at a higher level, and that after enrichment of this lake growth tended more to resemble that of fish in Lake Windermere although again at a much higher level.

It would appear that the chief result of the work carried out on this lake has been to show that a lake which was unproductive of animal life and capable of carrying only a limited stock of fish can, by suitable enrichment, be converted into a lake capable of carrying a much denser population of fish.

It does not follow that additions of fertilizer to lakes which already contain abundant plant and animal life, and are carrying an adequate stock of fish, will improve the size or condition of the fish.

Since this account was written, Smith (1955) has published the results of similar work in Canada. Chemical enrichment of a basically unproductive lake led to much improved growth of aquatic plants, plankton, bottom fauna, and fish. Experimental conditions and results in both investigations were similar.

VIII. ACKNOWLEDGMENTS

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APPENDIX I

RECORD OF FISH TAKEN FROM LAKE DOBSON, SHOWING SCALE READINGS, LENGTH, SEX, AND AGE

Date of Capture	Length for Each Year									At Capture		
	L_1 (cm)	L_2 (cm)	L_3 (cm)	L_4 (cm)	L_5 (cm)	L_6 (cm)	L_7 (cm)	L_8 (cm)	L_9 (cm)	L (cm)	Sex	Age
1945 *Year Class*												
19/v/1952	8.5	17.0	21.5	37.0	53.5	62.5	64.0			64.0	M	7
24/i/1954	10.0	18.5	23.0	30.0	37.5	42.5	48.5	56.5		60.0	F	8+
16/v/1954	13.5	26.0	37.0	41.0	43.0	46.0	52.5	63.5	65.0	65.0	M	9
1946 *Year Class*												
19/v/1952	10.5	25.0	40.5	48.5	52.5	57.0				57.0	F	6
1947 *Year Class*												
29/i/1954	16.5	24.5	28.5	36.5	48.0	52.5				54.5	M	6+
1948 *Year Class*												
21/i/1954	9.0	16.5	31.5	48.5	52.0					53.5	F	5+
23/i/1954	11.0	21.0	36.5	44.0	50.0					54.0	M	5+
24/i/1954	10.0	22.5	41.0	51.5	59.0					61.0	M	5+
18/v/1954	12.5	19.5	37.5	47.0	53.5	58.0				58.0	M	6
1949 *Year Class*												
20/i/1954	13.0	39.0	47.5	53.0						55.5	F	4+
22/i/1954	17.5	33.5	46.5	53.5						56.5	M	4+
22/i/1954	11.0	31.5	43.0	46.0						48.0	M	4+
24/i/1954	9.5	22.0	41.0	48.5						52.0	F	4+
29/i/1954	14.0	28.5	44.0	50.0						52.5	M	4+
16/v/1954	10.0	15.5	31.5	49.5	54.5					54.5	M	5

APPENDIX I (*Continued*)

Date of Capture	Length for Each Year									At Capture		
	L_1 (cm)	L_2 (cm)	L_3 (cm)	L_4 (cm)	L_5 (cm)	L_6 (cm)	L_7 (cm)	L_8 (cm)	L_9 (cm)	L (cm)	Sex	Age
1950 *Year Class*												
26/i/1954	11.5	26.5	36.5							40.5	F	3+
1951 *Year Class*												
19/i/1954	14.0	28.0								31.5	F	2+
	16.0	29.0								32.0	M	2+
	11.5	27.0								33.5	F	2+
	14.0	25.5								32.0	F	2+
	17.5	26.5								31.0	M	2+
	12.5	32.5								38.0	M	2+
20/i/1954	13.0	29.5								35.5	F	2+
	16.0	30.5								33.5	F	2+
21/i/1954	14.5	32.5								39.0	M	2+
23/i/1954	14.0	26.5								32.5	F	2+
	16.0	29.5								33.5	F	2+
	15.0	25.5								30.5	F	2+
	12.5	27.5								33.5*	M	2+
24/i/1954	14.5	30.5								36.0	F	2+
	15.5	26.5								32.0*	M	2+
25/i/1954	14.0	28.5								31.0*	M	2+
	19.0	*33.0*								*39.0*	*F*	*2+*
26/i/1954	13.5	31.0								39.5	M	2+
27/i/1954	13.5	30.0								37.0*	M	2+
	15.5	30.0								37.5	M	2+
	14.5	26.0								36.0	F	2+
29/i/1954	13.5	27.0								32.0	F	2+
	11.5	24.0								33.0	F	2+
30/i/1954	12.0	23.0								27.0*	M	2+
16/v/1954	16.0	32.5	37.5							37.5	†	3
	10.5	23.0	31.0							31.0*	†	3
	13.5	27.5	36.5							36.5	M	3
	10.5	25.0	33.0							33.0*	M	3
17/v/1954	13.0	26.0	33.0							33.0*	F	3
19/v/1954	14.5	28.0	38.0							38.0	M	3
	14.5	28.0	36.0							36.0	F	3
1952 *Year Class*												
16/v/1954	19.5	32.5								32.5	†	2
17/v/1954	—	30.0								30.0	M†	2
	17.5	30.0								30.0	M†	2
18/v/1954	20.0	31.0								31.0	M†	2

* Fish which had lost their tags; all the 1951 year class were tagged, hatchery-reared fish, except for the single rainbow of unknown origin, distinguished by numerals in italics.

† Fish released after examination; only sexually mature fish were sexed without dissection. Released fish were marked by the removal of the left pelvic fin. One fish of the 1952 year class was released without taking scales.

EXPLANATION OF PLATES 1 AND 2

PLATE 1

Lake Dobson from Mount Mawson, December 1952, showing the *Myriophyllum* clumps in the lines of the traverses made when bags of fertilizer were added in 1949. A similar response to the broadcast addition of fertilizer at the northern end in the following year is seen at the left. Eagle Tarn shows above this point.

PLATE 2

Fig. 1.—Scale from a male brown trout from Brady's Lake. This fish was 5 years old in May 1954; it measured 21¾ in. and weighed 5 lb 15 oz. Winter rings end at about 4½, 11¼, 14¾, 18¼, and 21¾ in. (Ref. 177; 7/v/1954; 10.)

Fig. 2.—Scale from male brown trout from Lake Leake. It was 5 years and 9 months old when taken in February 1954, 21 in. in length, and weighed 4 lb 8 oz. Winter rings end at about 5¼, 12¾, 16½, 19, and 20½ in. The rather indistinct second-year ring is characteristic of many lake fish. (Ref. M.4010.)

Fig. 3.—Scale from a male brown trout from Lake Dobson. This fish was 6 years and 8 months old when taken in January 1954. It measured 21½ in. and weighed 4 lb. Winter rings end at about 6½, 9½, 11¼, 14½, 19, and 20½ in. The scale shows the improved growth of the fish after its third year, corresponding with improved conditions in the lake from 1950 onwards. (Ref. 170; 29/i/1954; 71.)

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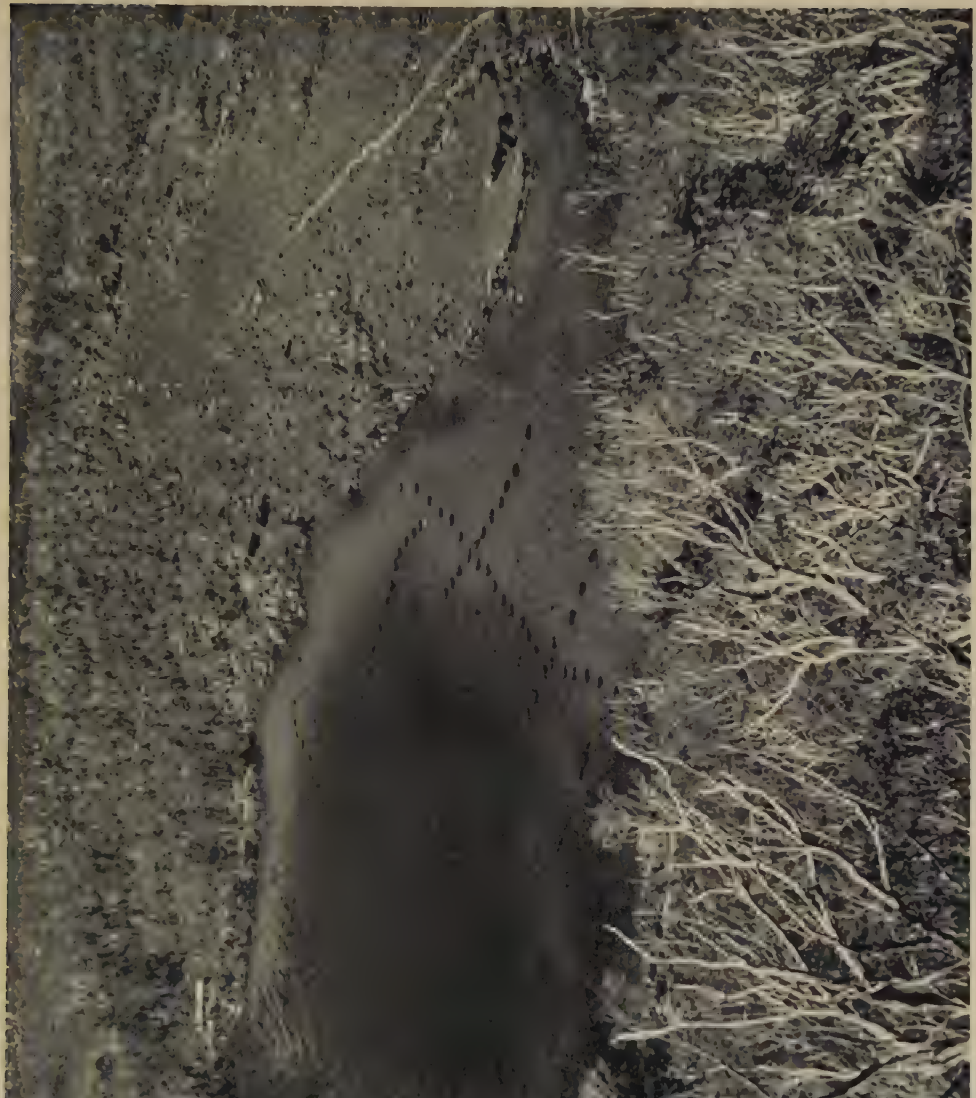

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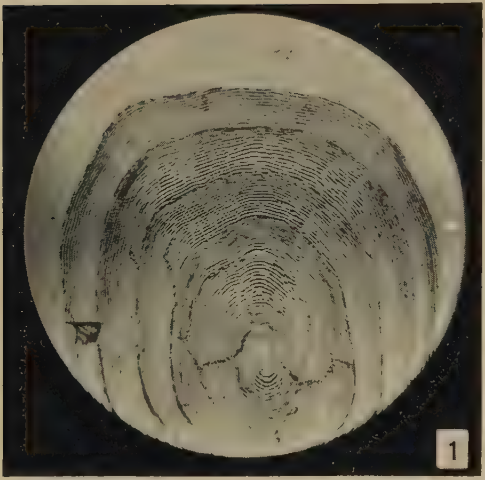
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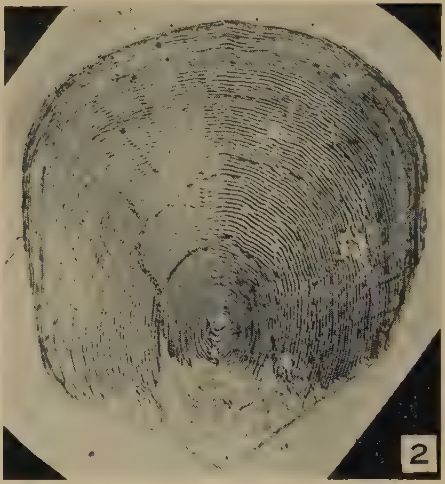
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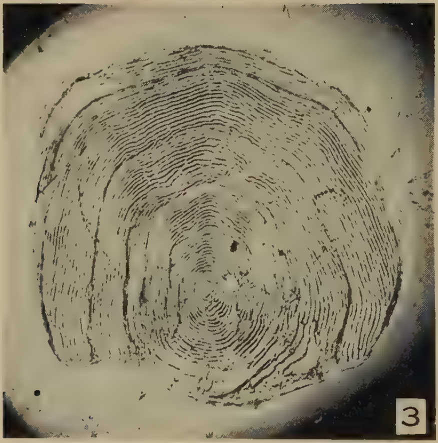
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OBSERVATIONS ON PERIODICITY IN MARINE INVERTEBRATES

By Barbara Dew* and E. J. Ferguson Wood*

(*Manuscript received October 18, 1954*)

Summary

Arising from field observations of marine fouling in Sydney Harbour, a study was made of planktonic larvae and fouling settlement to see whether the peculiar results observed in the field could be due to a tidal periodicity.

While not conclusive, there is evidence of periodicity which may be related to tides. Periodicity was observed in the distribution of lamellibranch and polychaete larvae in the plankton and in the settlement of *Balanus amphitrite* Darwin and *Hydroides norvegica* Gunnerus.

I. Introduction

It is now generally recognized that certain aspects of life are governed by a periodic rhythm, and often by a series of rhythms superimposed on each other, making difficult the recognition of each separate periodicity. Korringa (1947) describes a lunar or tidal periodicity in the spawning of the European oyster, *Ostrea edulis* L., in the Oosterschelde. He relates this to the spring tides rather than to the moon phase. In the same paper he reviews the literature on periodicity in marine organisms, and points to a large number of such organisms belonging to widely separated groups for which data suggesting lunar periodicity have been adduced. Loosanoff and Nomejko (1951) failed to find evidence of periodicity in the spawning of *Ostrea virginica* Gmelin, which, they state, commences spawning on June 30 ± 4 days. Imai (personal communication) considers that rising temperature acts as a trigger for the spawning of *Crassostrea gigas* Thunberg. However, it is not possible to specify either a temperature threshold or an approximate date for the commencement of spawning of Australian oysters, as Figures 3 and 4 show. These graphs show major spawning peaks for lamellibranchs (chiefly *Crassostrea commercialis* Iredale & Roughley) in early January 1951 and in February 1952. It would not be valid to use the findings of Loosanoff and Nomejko regarding *O. virginica* as a criticism of observations on periodicity of spawning in Australian oysters or the European oyster (see also Korringa 1952).

The work reported in this paper arose from an inspection by one of us (E.J.F.W.) of a sea-water cooling circuit. The inflow of this circuit consists of two identical conduits situated 50 ft apart, running from Darling Harbour, Sydney, to Ultimo power-house. The conduits had been cleaned 8 months prior to the inspection, the west conduit 14 days before the east conduit. The west conduit was heavily fouled with tube-worm, *Hydroides norvegica* Gunnerus, together with *Tubularia australis* Stechow, *Ciona intestinalis* L., etc. The east conduit contained a small amount of

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mussel fouling (*Mytilus planulatus* Lamarck), with *Balanus amphitrite* Darwin, a few hydroids (*Tubularia australis* and *Bougainvillia ramosa* van Beneden), and very small patches of *Hydroides norvegica.* The west conduit required immediate cleaning, while the east conduit could be left in service for many more months. We have frequently observed a marked antagonism between *Balanus* and *Hydroides* so that if one colonizes an area the other does not. Hence the biological significance of the fouling in this case lay in the fact that barnacles had settled first in one conduit, tube-worms in the other.

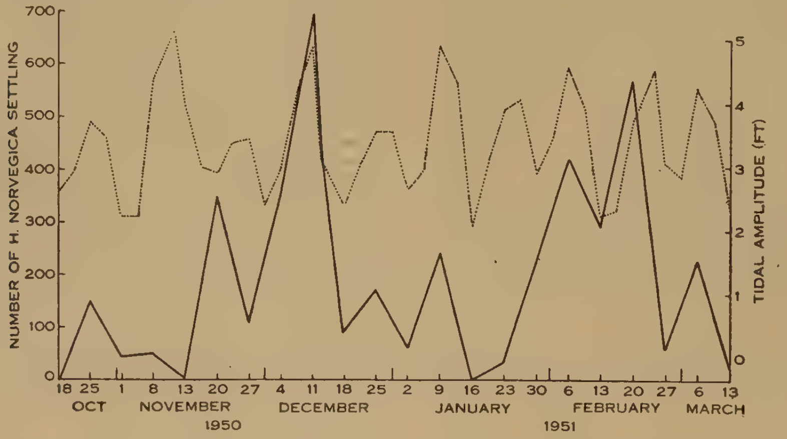

Fig. 1.—Settlement of *Hydroides norvegica* on plates exposed at weekly intervals at Darling Harbour, Port Jackson, 1950-51. Continuous line shows numbers of tube-worms and dotted line the tidal amplitude.

Because of the practical importance of these observations in regard to the cleaning of sea-water conduits and to ship docking schedules in Sydney Harbour, it was necessary to seek a biological explanation. Submerged glass panels had for some time been exposed at weekly intervals in Sydney Harbour, and the number of organisms settling thereon had been assessed. The results of these assessments for *Hydroides norvegica* are shown in Figure 1. It will be seen that there is, in general, a fortnightly periodicity in the settlement of *H. norvegica* on these panels, which coincides rather well with the spring tides. An interesting feature of this part of the investigation was the scarcity, and often the absence, of larvae of *Hydroides* from the plankton tows made at the time of these panel exposures. The cyprid larvae of *Balanus* were also rare in such tows. Other workers have also observed this phenomenon (Walton Smith, personal communication), but no explanation can be offered.

II. Experimental Field Studies

It was decided to make a series of daily plankton tows in Port Jackson, starting in October 1950, in order to find out whether a periodicity could be observed in the spatting and larval stages of fouling organisms. In the part of Sydney Harbour chosen for the work there are no marked tidal currents. Further, duplicate tows made in Athol Bight on the north side of the harbour, and east of Garden Island on the south side, showed no significant differences in numbers of larvae, so it was assumed that the values obtained were representative of that part of Sydney Harbour. As lamellibranch larvae preponderated in the plankton tows, the curves shown in this paper (Figs. 2-4) represent the total number of lamellibranch larvae. These were chiefly *Crassostrea commercialis*. Some information was also obtained regarding polychaete larvae, and though these were few the results in general confirmed those for the lamellibranchs.

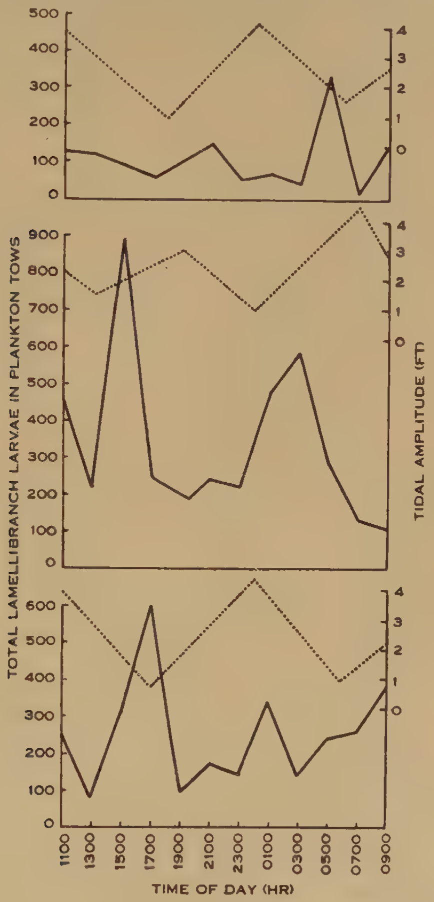

Fig. 2.—Two-hourly tows on three occasions at different points, showing rise and fall in the number of lamellibranch larvae over 24-hr periods. Dotted line shows tidal movement.

An attempt was made to determine the species of the larval lamellibranchs, but the earlier stages were difficult or impossible to identify, while the separation of the older larvae into species did not significantly affect the curves. Moreover, such separation meant the omission of the very young stages. It is realized that larvae may suffer many vicissitudes between spawning and settlement, that settlement may be spread over a period, and that it is not possible, in field experiments, to allow for all the factors involved. One factor—temperature—was considered, but the changes and range were not such as to affect the larvae to any appreciable extent, nor could temperature be correlated with counts of larvae.

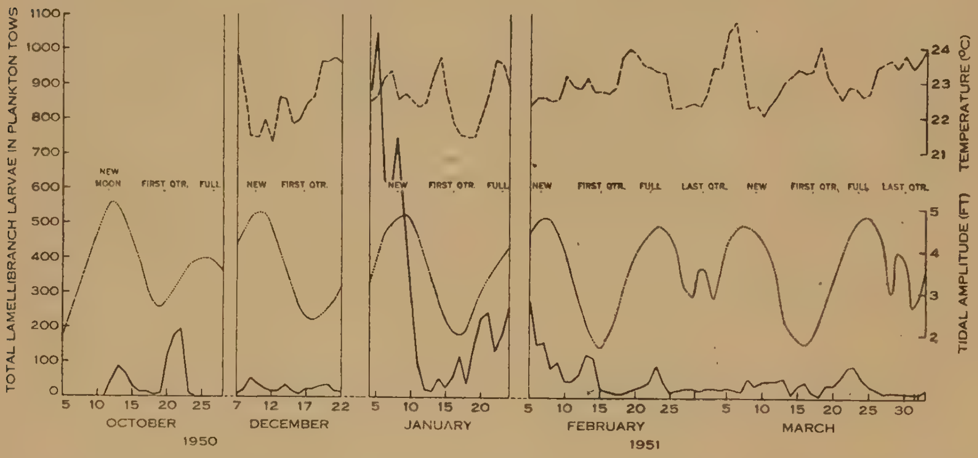

Fig. 3.—Counts of lamellibranch larvae in Port Jackson for a discontinuous period between October 1950 and April 1951 (continuous line), showing relations with tidal amplitude (dotted line). Water temperature is shown by broken line.

In the first series of experiments, which extended from October 1950 to early April 1951, with certain unfortunate breaks, tows were made using nets with a 6½ in. diameter ring, and silk with 150 meshes per inch. Tows were made at high and low water, and at 1 m and 15 m depth, i.e. eight samples a day, approximately half a mile from shore, and with a depth of water of upwards of 17 m at low tide. A towing speed of approximately 2 knots was maintained for 20 min, 10 min with and 10 min against the wind. The catches were concentrated to 50 ml and aliquots taken, or if the organisms were few the whole tow was counted. The results for each day are averaged in the graphs (Fig. 3), though statistical analyses of day and night tows, surface and deep tows, and tows at high and low tide were also made.

Because of statistically significant differences between day and night tows, tows were made at 2-hr intervals for 24 hr on several occasions in 1951-52. Figure 2 shows some of the counts for such tows. There appear to be three maxima daily, these occurring between 9 and 11 a.m., in the afternoon, and after midnight, though there is some irregularity of time which does not correspond with tide. As one of the peaks occurs during the day, the cause cannot be insolation.

As the time of day, therefore, seems to be of more significance in the plankton catches than the state of the tide, the daily tows were repeated in the summer of 1951-52 at fixed hours, 9 a.m. and 9 p.m., and with greater continuity on this occasion, due to the availability of a more reliable craft. The tows were made, and the results obtained in the same manner as those of the previous season (Fig. 4).

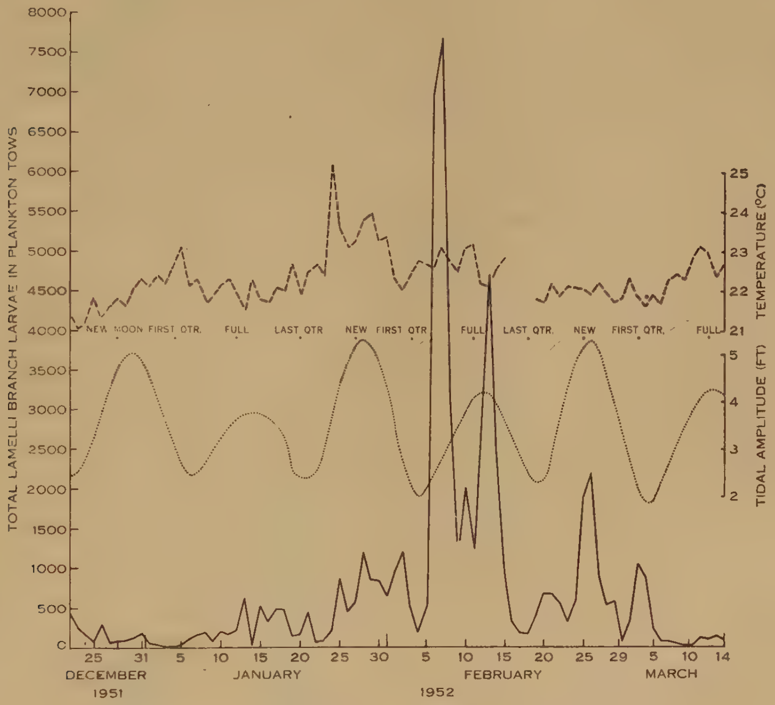

Fig. 4.—Counts of lamellibranch larvae in Port Jackson between December 1951 and March 1952 (continuous line) showing relationships with tidal amplitude (dotted line) and temperature (broken line).

The averaged results of the 1950-51 tows are shown in Figure 3, and those of the 1951-52 tows in Figure 4. There is a periodic rhythm coinciding fairly well with spring tides, although there is at least one other rhythm of unknown cause superimposed on the tidal one. In the lamellibranchs, this seems from statistical analyses to be an 18-day rhythm, and in polychaetes a 12-day one, but in neither case was the rhythm well defined.

Glass panels placed in racks (Allen and Wood 1950) suspended from buoy No. 7 off Garden Island (cruiser buoy) were exposed during the period of the 1951-52 tows. Plates were inserted daily and left in the rack for 7 days, thus giving a daily indication of the attachment of *Balanus amphitrite* and *Hydroides norvegica*.

These results (Figs. 5 and 6) also show a periodicity which seems to be related to the spring tides, and the graphs show some similarity to those of the plankton tows.

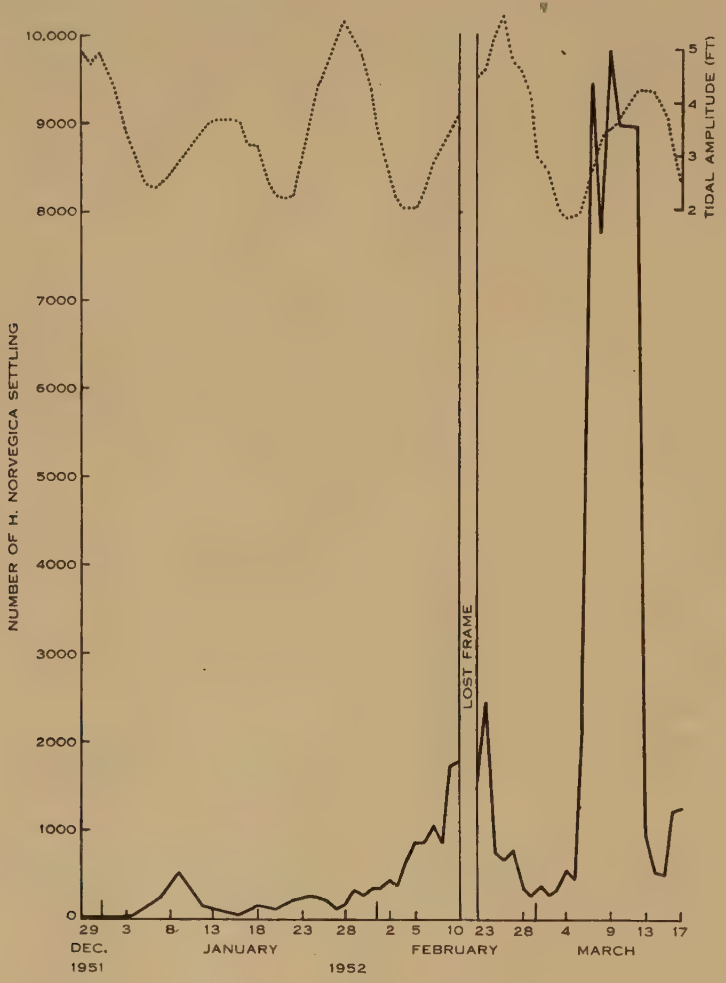

Fig. 5.—*Hydroides norvegica* attaching to submerged panels at Double Bay, December 1951-March 1952. Panels were exposed at 24-hr intervals for 7 days each.

In order to determine whether the observed periodicity could be correlated with lunar or tidal phenomena, plates were exposed and tows made simultaneously and in the same manner in Sydney Harbour and the Swan River, W.A. The Swan River has little tide, the water level depending on the prevailing winds and on rainfall. It was found that the peaks of occurrence of polychaete and lamellibranch larvae in the Swan River did not coincide with those in Sydney Harbour (compare Figs. 3 and 8), and it was assumed therefore that they could not be lunar. Figure 7 shows the water level and the attachment of *Bugula avicularia* Pallas and *Spirorbis* sp. to glass slides in the Swan River. In both Figures 7 and 8 there seems to be some relationship between tidal height and both plankton counts and attachment of organisms, with a lag of approximately 4 days, but the relationship is not clear-cut.

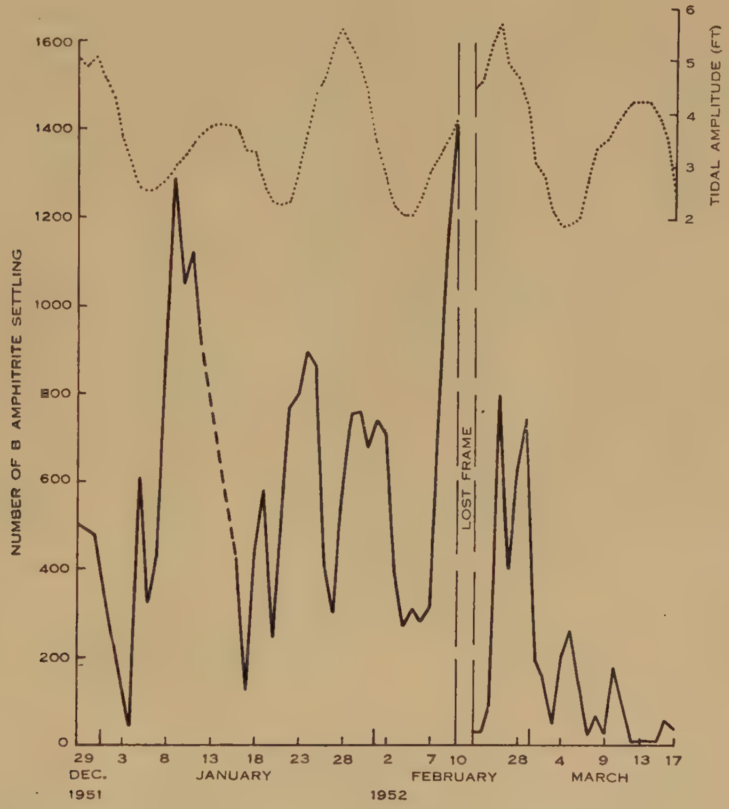

Fig. 6.—*Balanus amphitrite* attaching to submerged panels at Double Bay, December 1951-March 1952. Panels were exposed at 24-hr intervals for 7 days each.

III. Discussion

Although the evidence is not as clear as was desired, it does, on the whole, seem to support Korringa's (1947) theory that there is a relation between spawning of certain fouling organisms and tidal amplitude. Conclusive evidence is difficult to obtain, as observations would have to be more frequent and continuous than is possible. Moreover, field evidence would have to be corroborated by aquarium studies, in order to eliminate some of the variables. There is no evidence of an innate rhythm in the curves for Swan River and Sydney Harbour (Figs. 3 and 8).

The results obtained in this survey for deep and surface tows (see Table 1) suggest that the larval swarms appear suddenly at or near the bottom, and become diffused throughout the water mass.

It would appear that the larvae, when released, sink rapidly to the bottom (trochospheres were very rare), possibly owing to positive geotropism, and rise and are dispersed at a certain stage owing to a change in geotropism, a phenomenon already recorded in the literature. Because the larval bursts seem to follow closely after the neap tides and reach a maximum at the springs, it may well be that these bursts are caused by low rather than by high pressures, or by a lowering followed by a rising of pressure.

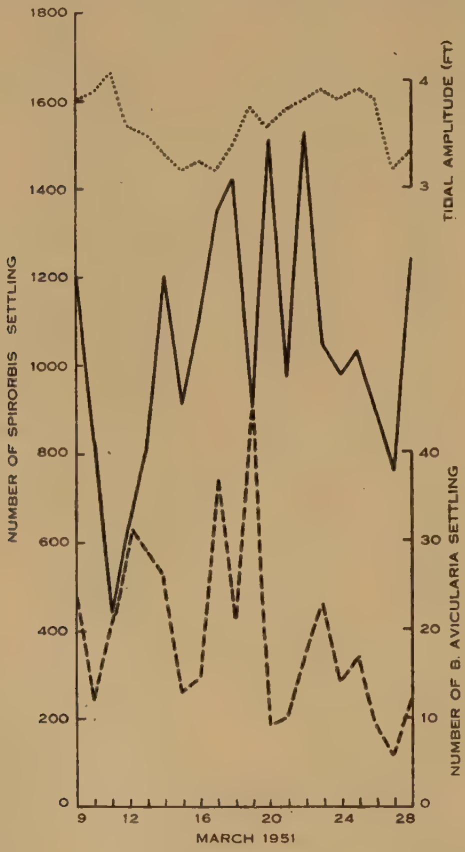

Fig. 7.—Attachment of *Spirorbis* (continuous line) and *Bugula avicularia* (broken line) to submerged panels (7-day exposure at 24-hr intervals) in the Swan River, W.A. Tide level is shown by dotted line.

Throughout the survey considerably more larvae of lamellibranchs and polychaetes were found in the deep than in the surface tows, though, as Table 1 shows, the ratio of numbers of larvae in deep and surface tows varies from day to day. In February 1952 (the spawning peak), statistical analysis showed that there were significantly more lamellibranch larvae in the night than in the day tows (Table 2). Polychaetes were always more numerous in the night than in the day tows (Table 3).

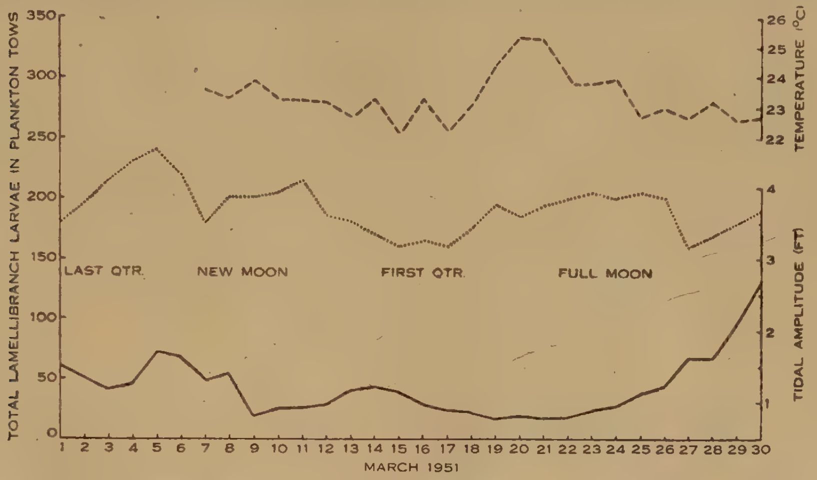

Fig. 8.—Lamellibranch larvae in plankton tows in the Swan River, W.A. (continuous line), showing tide level (dotted line) and water temperature (broken line).

TABLE 1

APPEARANCE OF LARVAE IN SYDNEY HARBOUR PLANKTON DURING PEAKS IN FEBRUARY 1952

	Daily Counts									
Tows	Feb. 5	6	7	8	9	24	25	26	27	28
Surface	83	108	201	514	204	82	204	287	266	242
Deep	45	1044	1400	337	238	96	330	671	349	167

TABLE 2

LARVAL LAMELLIBRANCHS

Means of log $(N + 1)$, where N is the number of larvae

Time of Day	Tow	Dec.	Jan.	Feb.	Mar.	Total Period
Day	Surface	1.222	1.197	1.611	1.241	1.350
	Deep	1.474	1.506	1.831	1.309	1.582
	Mean	1.348	1.352	1.721	1.275	1.466
Night	Surface	1.240	1.210	1.856	1.266	1.446
	Deep	1.334	1.462	1.961	1.400	1.609
	Mean	1.287	1.336	1.908	1.333	1.527
Mean	Surface	1.231	1.204	1.733	1.254	1.398
	Deep	1.404	1.484	1.896	1.355	1.596
	Mean	1.317	1.344	1.815	1.304	1.497

These differences between the numbers of larvae in deep and surface tows, and in night and day tows, are bound up with changing geotropism, phototropism, and possible barotropism of the larvae.

TABLE 3

LARVAL POLYCHAETA

Means of log $(N + 1)$, etc. where N is the number of larvae

Time of Day	Tow	Dec.	Jan.	Feb.	Mar.	Total Period
Day	Surface	0.422	0.089	0.237	0.115	0.186
	Deep	0.581	0.396	0.485	0.257	0.430
	Mean	0.501	0.243	0.361	0.186	0.308
Night	Surface	0.590	0.395	0.630	0.486	0.515
	Deep	0.752	0.467	0.700	0.493	0.588
	Mean	0.671	0.431	0.665	0.489	0.551
Mean	Surface	0.506	0.242	0.433	0.300	0.350
	Deep	0.666	0.432	0.592	0.375	0.508
	Mean	0.586	0.337	0.513	0.338	0.429

IV. CONCLUSIONS

There were never enough cyprid larvae in the tows for conclusions to be drawn, but it is possible that the difference in the fouling of the conduits at Ultimo was due to the effects of periodicity. The practical application of this work depends on the coincidence of the main larval bursts and subsequent settlement with the spring tides. It would seem inadvisable to clean sea-water lines or undock ships near spring tides, if this can be avoided, while exposure of culture material for catching mussel or oyster spat should be made close to such periods.

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